

FITNESS COSTS AND BENEFITS OF EGG EJECTION BY GRAY CATBIRDS

BY

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A thesis presented to the University of Manitoba
in fulfillment of the thesis requirements for the degree of
Master of Science in the Department of Zoology

Winnipeg, Manitoba
Janice C. Lorenzana
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Fitness Costs and Benefits of Egg Ejection by Gray Catbirds

BY

Janice C. Lorenzana

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University
of Manitoba in partial fulfillment of the requirements of the degree**

of

MASTER OF SCIENCE

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ABSTRACT

The objective of this study was to identify selective pressures for egg ejection in Gray Catbirds (*Dumetella carolinensis*). Two possible selective pressures were tested: brood parasitism by conspecifics and by Brown-headed Cowbirds (*Molothrus ater*). Catbirds accepted all 27 foreign catbird eggs placed into their nests, and conspecific brood parasitism was not detected in 95 catbird nests that were monitored during the egg-laying stage. Conspecific brood parasitism, therefore, did not select for egg ejection in Gray Catbirds. The hypothesis that parasitism by the Brown-headed Cowbird selected for egg ejection predicts that the cost of accepting a cowbird egg is greater than the cost of ejecting it. The cost of ejecting cowbird eggs was determined by adding a model cowbird egg to catbird nests to quantify the frequency with which catbirds damaged or ejected one or more of their own eggs along with the parasitic egg. The cost of ejection for catbirds was 0.01 catbird eggs per ejection, which is the equivalent of 0.0022 catbird fledglings per ejection. I determined the cost of acceptance by placing cowbird chicks into catbird nests. A mean of 0.63 fewer chicks fledged from parasitized nests than from unparasitized nests. Therefore, it is adaptive for catbirds to eject foreign eggs because the cost of accepting a cowbird chick is much greater than the costs of ejecting cowbird eggs. Parasitism by the cowbird, therefore, provides selective pressure for ejection behaviour in catbirds.

Cowbird chicks received more than twice as much food as catbird chicks even though they are not much larger relative to catbird chicks. Height rank was found to be the single most important parameter that determined which nestling is offered food. Cowbirds reached higher than catbird chicks simply because they were larger and not because they begged more intensely (i.e., both cowbird and catbird chicks generally only stretched their necks when they begged and did not extend their tarsi). The female adult

catbird increased its provisioning rate in parasitized nests, which reduced the effect of the presence of the cowbird chick on the amount of food obtained by catbird chicks. The increased provisioning rate of the adult females may be indicative of an additional, immeasurable cost of parasitism, namely a reduction in the survival and lifetime reproductive success of the adult female.

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GENERAL INTRODUCTION

Brood parasitism is a reproductive strategy in which birds lay some or all of their eggs in nests of unrelated individuals, and leave the care of their offspring entirely to the hosts. Brood parasites may employ a facultative strategy in which the birds raise their own broods, but also lay some of their eggs in the nests of other birds, or an obligate strategy in which individuals exclusively parasitize other species. Facultative parasites may lay in nests of conspecifics (conspecific or intraspecific brood parasitism, Yom-Tov 1980) or other species (interspecific brood parasitism). Obligate brood parasites may specialize on one or a few host species, or they may be generalists, capable of parasitizing hundreds of species. There are 96 species of obligate brood parasites, including a duck (Anatidae), cuckoos (Cuculidae), honeyguides (Indicatoridae), cowbirds (Icteridae), and finches (Ploceidae) (Ortega 1998:8). The Brown-headed Cowbird (*Molothrus ater*), an obligate brood parasite with a generalist strategy, is the focus of the present study. The cowbird has been recorded parasitizing 226 species (Ortega 1998:183). Of these, 132 species are biological hosts, species that are regularly parasitized and also raise cowbirds (Ortega 1998:184). The cowbird's historical range once was limited to the Great Plains, but now spans most of North America as a result of the clearing of forests and the development of agriculture in the last century (Mayfield 1965, Rothstein et al. 1980, Rothstein 1994).

Nests parasitized by cowbirds often produce fewer host offspring than unparasitized nests (e.g. Payne 1977; Lorenzana and Sealy, in press). Hosts, therefore, should evolve antiparasite defenses. Host defenses include nest concealment (Burhans 1997), nest defense (Neudorf and Sealy 1992, Gill and Sealy 1996, Strausberger and Horning 1998), nest desertion (Petit 1991, Hill and Sealy 1994), egg burial (Clark and Robertson 1981, Sealy 1995, Mico 1998) and egg ejection (e.g., Rothstein 1975a,

1982b, 1990). Ejection is the only behaviour, however, that may be clearly interpreted as an evolved antiparasite strategy because the other behaviours also occur outside the context of brood parasitism. It should never be adaptive for birds to eject their own eggs, unless they are broken (Kemal and Rothstein 1988). Egg ejection most effectively allows hosts to eliminate the costs of raising a cowbird because the parasitic egg is targeted specifically; nest desertion and burial usually also eliminate the host's own eggs. Surprisingly, egg ejection has evolved only in 10% of the cowbird's biological hosts (Ortega 1998:20, 183-184).

The response of potential hosts to parasitism may be determined experimentally by recording the response of nest-owners to a model cowbird egg added to their nests. Rothstein (1975a) found that cowbird hosts either accept or reject cowbird eggs at a frequency close to 100% (but see Haas and Haas 1998). The Gray Catbird (*Dumetella carolinensis*), hereafter catbird, is one such ejecter species (Rothstein 1975a). Like other ejecter species, catbirds show true egg recognition and specifically eject foreign eggs from their nests, rather than ejecting the egg that differs from the other eggs in a clutch (Rothstein 1975b). Furthermore, Rothstein (1974) demonstrated that catbirds learn to recognize their eggs through an imprinting process, rather than possessing an innate recognition of their eggs.

Catbirds are sympatric with cowbirds over most of the former's range and they have been parasitized at a frequency as high as 44% (Scott 1977). The parasitism frequency of ejecter species may be underestimated if a cowbird egg is ejected before it can be detected during nest inspections by investigators. Scott (1977) minimized this source of error by checking catbird nests daily around dawn, when cowbirds lay their eggs (Scott 1991). At Delta Marsh, Manitoba, where the present study was conducted, about 5% of catbird nests were parasitized (Neudorf and Sealy 1994). Many cowbird hosts are much smaller than the cowbird (Lorenzana and Sealy, in press). Adult

catbirds are 95% of the mass of female cowbirds and 75% of the mass of male cowbirds (calculated from adult masses obtained from Dunning 1993); therefore, catbirds (36.9 g) are large relative to other hosts. Nevertheless, catbirds are one of the smallest ejecter species; at 15 g, only the Warbling Vireo (*Vireo gilvus*) is smaller.

I investigated two possible selective pressures for egg ejection behaviour in catbirds: conspecific brood parasitism and cowbird parasitism (Chapter 1). To test whether conspecific brood parasitism was an important selective pressure, the frequency of conspecific brood parasitism in catbirds was determined. Secondly, catbird eggs were added to nests to determine whether catbirds recognize and eject them. To test whether cowbird parasitism was an important selective pressure, the costs and benefits of ejection of cowbird eggs were determined. The cost of ejection was determined by adding model cowbird eggs to catbird nests and recording the frequency with which catbird eggs disappeared along with the cowbird egg. Missing catbird eggs probably were accidentally damaged and/or accidentally ejected during the ejection process. The benefit of egg ejection was determined by quantifying the cost of rearing a cowbird chick in terms of its effects on host fledging success and nestling size.

I explored a type of cost of parasitism that was not easily quantifiable, namely a decrease in the survivorship and lifetime reproductive success of catbirds (Chapter 2). One reason why the lifetime survivorship of hosts may decrease as a result of parasitism is that adults may work harder to provision nests that contain a cowbird chick (Furrer *in* Friedmann et al. 1977). Catbird nests were videotaped to determine whether parental feeding rates are greater at parasitized than at unparasitized nests. If catbird adults must augment their feeding rates to feed an additional cowbird chick, this may lead to decreased survivorship and lifetime reproductive success of catbird adults (Stearns 1992).

The competitive interactions between catbird nestlings and the unrelated cowbird nestling were analyzed (Chapter 3). Investigation of how cowbird chicks compete with catbird chicks provides knowledge of the mechanism by which cowbird chicks may affect the fledging success and growth of catbird chicks.

STUDY SITE

This project was conducted from mid-May to early July in 1996 to 1998 at Delta Marsh, Manitoba (50°11'N, 98°19'W). Catbird nests were found along a 10-km strip of the dune ridge forest that runs along the southern shore of Lake Manitoba on the properties of the University of Manitoba Field Station (Delta Marsh), the Portage Country Club, Delta Beach cottage area, and the Delta Waterfowl and Wetlands Research Station. MacKenzie (1982) and Neudorf (1991) provide detailed descriptions of the study area. Catbirds nest close to the ground, with a mean height of 1.5 m in dense, shrubby vegetation (Cimprich and Moore 1995). Marcus (1973) provided a list of plant species used as nest sites at Delta Marsh.

Chapter 1. Selective pressures for egg ejection in Gray Catbirds

Given that there are often fitness costs for hosts to raise young of the parasitic Brown-headed Cowbird (e.g., Payne 1977; Lorenzana and Sealy, in press), hosts should evolve defenses that eliminate parasitism or minimize its impact. The most effective antiparasite strategy is egg ejection because the parasitic egg is targeted and the rest of the clutch is left intact, unlike nest desertion and egg burial where the entire clutch may be lost. Egg ejection requires a bird not only to recognize a foreign egg in its nest, but also physically to remove it. The requirement for both of these abilities may account for egg ejection having evolved in only 10% of the Brown-headed Cowbird's biological hosts (Ortega 1998:20, 183-184). In many studies, the mechanisms of egg recognition by ejecters have been studied (e.g., Rothstein 1974, 1975c, 1977, 1978, 1982a), but few have quantified the selective pressure for egg ejection. This may be because if parasitism is costly for hosts that accept cowbird eggs, it must also be costly for ejecter species.

Nonetheless, it should be demonstrated that parasitism exacts a cost on ejecter species. Ejecters are often large hosts, which may incur a lower cost than for smaller hosts (Lorenzana and Sealy, in press). In two studies where the costs of parasitism on ejecter species were quantified, there was no statistically significant cost of parasitism (Bullock's Oriole, *Icterus bullockii*, Røskaft et al. 1993; Brown Thrasher, *Toxostoma rufum*, Haas and Haas 1998). Although, Røskaft et al. (1993) did not find a significant cost of parasitism, they concluded that selection favours ejection behaviour in Bullock's Orioles because the cost of parasitism for a brood size of four chicks (0.40 oriole chicks) was greater than the cost of ejection (0.26 oriole eggs). With such a small difference between the cost of acceptance and cost of ejection, one wonders whether this difference is biologically significant, especially given that a significant cost of parasitism

was not found. To date no one has demonstrated experimentally that parasitism by the Brown-headed Cowbird is the selective pressure for the evolution of egg ejection behaviour in any species. If cowbird parasitism is essentially cost free, an alternate explanation for the evolution of egg ejection is required. Perhaps egg ejection evolved in response to brood parasitism in an ancestral population or species and was maintained through speciation events (Baltz and Burhans 1998). Alternatively, egg ejection may have evolved in response to parasitism by a large brood parasite in the past (Peer 1998).

In this study, I examined possible selective pressures for egg ejection in the Gray Catbird, the smallest known grasp-ejecter of cowbird eggs. Four conditions are known to select for ejection of foreign eggs by birds: 1) colonial nesters that may confuse their eggs with those of conspecifics, 2) conspecific brood parasitism, 3) interspecific brood parasitism, and 4) nest usurpation where species lay their eggs in nests of others before ejecting the original nest-owners' eggs (Peer and Bollinger 1998). Catbirds are not colonial nesters and do not usurp nests; therefore, the potential selective pressures of conspecific brood parasitism and interspecific brood parasitism were tested. The hypothesis that conspecific brood parasitism selects for egg ejection in Gray Catbirds was tested by adding a single catbird egg to a catbird clutch or by replacing a single catbird egg with a foreign catbird egg. By the conspecific brood parasitism hypothesis, it was predicted that catbirds regularly lay their eggs in the nests of other catbirds, and that catbirds eject the foreign catbird eggs.

The hypothesis that parasitism by the Brown-headed Cowbird selects for egg ejection in Gray Catbirds predicts that acceptance is more costly than rejection. The cost of ejecting cowbird eggs was quantified by adding a model cowbird egg to catbird nests to quantify the frequency with which catbirds ejected one or more of their own eggs when ejecting the cowbird egg. Davies and Brooke (1988) identified two costs of

egg ejection: 1) a recognition cost (own egg ejected *instead* of parasitic egg), and 2) an ejection cost (own egg ejected *along* with parasitic egg). The recognition cost may occur even in the absence of parasitism (Lotem and Nakamura 1998). The recognition cost is normally associated with parasitic eggs that are similar in appearance to host eggs and is highly unlikely to apply to the ejection of cowbird eggs by catbirds because cowbird and catbird eggs are different. Cowbird eggs have white ground colour with specks, whereas catbird eggs are bluish-green with no spotting. Ejection costs may occur when a host egg is damaged during the ejection of the parasitic egg, and the damaged egg is subsequently removed, or simply ejected by mistake.

Costs of parasitism in light of the evolution of egg ejection are either recoverable or non-recoverable. Costs are recoverable if they are eliminated when a cowbird egg is ejected, whereas they are non-recoverable if they are incurred regardless of whether a cowbird egg is ejected (Røskaft et al. 1990). Egg ejection would be selected only if recoverable costs of parasitism were greater than the cost of ejection. The cost of accepting a cowbird egg is equal to the recoverable cost of parasitism, and in this study, was calculated as the differential fledging success between experimentally parasitized and unparasitized broods. Examples of recoverable costs include reduced host egg hatchability and brood reduction due to competition with the cowbird chick. A non-recoverable cost is removal of host eggs by the parasite (Røskaft et al. 1990).

Scott et al. (1992) estimated that female cowbirds remove at least 0.80 host eggs per cowbird egg laid in a variety of different host species. Host egg removal may benefit the cowbird by increasing the fledging success of cowbirds and reducing the cost of parasitism on the remaining catbirds in the nest. In essence, host egg removal may reduce the *recoverable* cost by increasing the *non-recoverable* cost (i.e., host egg removal). If the recoverable cost is reduced enough such that it is lower than the cost of

ejection, it may prevent evolution of antiparasite strategies. Because host egg removal occurs in naturally parasitized catbird nests (Scott 1977), host egg removal was simulated in this study by removing a catbird egg from some nests that received a cowbird chick.

METHODS

Catbird nests were located at Delta Marsh, Manitoba from 1996 to 1998, with more extensive nest-searching in 1997 and 1998. See General Introduction for more information about the study site. Thirty-six catbird nests were found in 1996, 111 in 1997, and 131 in 1998. In 1996, nests were checked at least every second day for 5 to 7 days after the addition of a conspecific egg to the nest. In 1997, nests were checked every day from the day they were found to 8 days after hatching, with the exception that during mid- to late incubation, nests were checked every other day. In 1998, nests were checked every day until fledging, with the exception of mid-incubation over a period of 8 days when they were not checked at all.

Egg addition experiments

Conspecific egg additions

Real catbird eggs were added to catbird nests in 1996 during laying and the first five days of incubation. Single catbird eggs were switched between pairs of catbird nests that were close to the same stage of development (see Lanier 1982), or a real catbird egg was added to a catbird clutch without removing any eggs from the original clutch (see Bischoff and Murphy 1993). Switching catbird eggs simulated host egg removal, a behavior that is known to occur in some species that practice conspecific brood parasitism (e.g., Brown and Brown 1988, Lombardo et al. 1989). All catbird eggs added to nests were marked with a nontoxic marker. Nests were then checked at least

every second day for at least six days after the introduction of the foreign egg. Following Rothstein's (1975a) definition, a foreign egg was considered ejected only if it disappeared from an otherwise active clutch. It was considered accepted if it remained in the active nest for at least six days. A six-day acceptance criterion was used because less than 1% of rejections occur after 5 days (Rothstein 1982a).

In 1997 and 1998, the frequency of natural conspecific brood parasitism was determined by recording the appearance in a nest of more than one new catbird egg per day during the laying stage or the appearance of an egg during the incubation or nestling period. Catbirds lay only one egg per day (Cimprich and Moore 1995). Eggs were numbered with a non-toxic marker on the day they were laid to detect the replacement of a catbird egg by a foreign egg.

Cowbird egg additions

Experiments involving model cowbird eggs were conducted in 1997. Model eggs were made of plaster-of-Paris from casts of real cowbird eggs and painted with acrylic paints and polyurethane to mimic real cowbird eggs (as in Rothstein 1975a). Model eggs have been used successfully in many studies of host responses to brood parasitism (e.g., Rothstein 1975a, Davies and Brooke 1989, Hill and Sealy 1994). All cowbird eggs were added before noon. Catbird nests found early in the nesting stage were parasitized with one model cowbird egg on LD2 (i.e., the day the second catbird egg was laid). Nests found after LD2 were parasitized on LD5 or during early incubation. Catbird eggs were numbered as they were laid to permit detection of partial predation during the egg-laying stage and to determine whether conspecific brood parasitism occurred.

Nests were checked five hours after parasitism and every morning thereafter until the cowbird egg was ejected. Ejection was recorded when the cowbird egg was

missing, and acceptance was recorded when it remained in an active nest for at least six days. When one or more host eggs were gone, along with the model cowbird egg, but the nest remained active, this was considered ejection with a cost. This inference has been used by others (Rohwer et al. 1989, Sealy and Bazin 1995, Sealy and Neudorf 1995, Sealy 1996). Because eggs missing during ejection could also be due to partial predation, background rates of partial predation in 1996 were calculated to compare with the number of eggs missing during ejection of model cowbird eggs in 1997.

Cost of acceptance

Estimating the cost of accepting a cowbird egg must be done by experimentally placing newly hatched cowbird chicks into catbird nests because catbirds eject almost all cowbird eggs naturally or experimentally placed into their nests. The success of this experiment required that catbirds accept cowbird chicks. No ejecter species are known to eject foreign nestlings (e.g., Lotem 1993, Lotem et al. 1995, McLean and Maloney 1998). Furthermore, catbirds naturally parasitized occasionally rear cowbird chicks (e.g. Nickell 1958, McGeen and McGeen 1962, Lowther 1980).

Nests of commonly parasitized acceptor species (Appendix 1) were monitored for cowbird eggs. All cowbird eggs found when catbird clutches were being initiated were collected and incubated artificially to eliminate the risk of loss to predators. Cowbird eggs collected before the first catbird clutches were initiated were refrigerated at 10 °C until they needed to be incubated. Low temperatures arrest embryonic development and extend the embryo's viability (Drent 1975). To maximize the number of cowbird eggs collected, female cowbirds were captured in baited tunnel traps and fed and maintained in cages for a maximum of three mornings, and any eggs laid during this time were collected and artificially incubated (methods follow McMaster and Sealy 1997). Eggs in the incubator were turned four times daily to prevent embryonic membranes from

adhering to the shells, and candled and massed every two days to track embryo development. The numbers of cowbird chicks obtained from each nest type and from the female holding cages are given in Appendix 1.

One newly hatched cowbird chick was placed into each experimental nest, whereas no chicks were added to control nests. In 1997, no catbird eggs were removed from experimental nests. In 1998, a catbird egg was randomly removed from half of the experimental nests to simulate host egg removal by the female cowbird (e.g. Sealy 1992). In 1997, cowbird chicks were placed in randomly chosen catbird nests on the same day that the first catbird chicks hatched. In 1998, I attempted to place cowbird chicks into nests on the day before catbird chicks were predicted to hatch because cowbirds usually hatch one day earlier than catbird chicks. The mean incubation period for the catbird, defined by Nice (1954) as the time between the laying of the last egg and the hatching of the last nestling, is 12.9 days (Johnson and Best 1980). The mean incubation period for the cowbird, defined by Briskie and Sealy (1990) as the time from the start of full incubation by the host to hatching, is 11.9 days. Full incubation in catbirds begins when the clutch is complete or nearly complete (Johnson and Best 1980). Cowbirds generally parasitize nests before the clutch is complete (e.g. Sealy 1995); therefore, cowbirds should hatch the day before any host eggs hatch. Because there was variability in the length of time catbirds took to hatch, cowbird chicks were normally added 1 to 2 days before the first catbird chick hatched, but sometimes up to 4 days elapsed before the first catbird chick hatched. The mean \pm SE number of days the cowbird was added to the nest before first catbird chick hatched was 1.7 ± 0.2 ($n = 27$).

Catbird chicks were individually colour-marked with a non-toxic felt pen so that the development of each could be tracked. The length of the left tarsus and mass of all chicks were measured daily. According to Rising and Somers (1989), tarsus length

appropriately estimates body size because it approximates many multivariate measures. Chicks were not measured past day 8 (where day 0 is the day the first catbird chicks hatched) because handling chicks after this age may cause them to fledge prematurely (pers. obs.). The number of catbird chicks that fledged was defined as the number of chicks present in the nest at 8 days post-hatch in 1997. In 1998, nests were monitored until all chicks fledged.

DATA ANALYSES

SPSS version 8.0 was used to perform all statistical analyses. An alpha of 0.05 was used in all statistical tests. When testing more than one factor effect, a significance level (α_i) was calculated to ensure that the family level of significance did not exceed 0.05 using the Kimball inequality, $\alpha \leq 1 - (1 - \alpha_i)^i$, where i = number of main effects and interactions (Neter et al. 1990:710, 841). All p-values were then modified such that $\alpha_i = 0.05$ to facilitate the interpretation of the p-values.

Cost of ejection

Cost of ejection was calculated as the number of catbird eggs that went missing during the same time period that the cowbird egg went missing minus the partial predation rate at unparasitized nests. Partial predation rate was the number of catbird eggs that went missing per day that a nest was checked during the egg stage in 1996, when model cowbird egg manipulations were not performed. The cost of ejection and the cost of rearing a cowbird chick needed to be in the same units before they could be compared. Eggs are not as valuable as fledglings because the embryos within the eggs have a lower probability of fledging. The cost of ejection was, therefore, devalued by 22.1%, which is the mean percentage of catbird eggs from which chicks fledged in nests that did not receive a cowbird chick ($n = 204$).

Cost of acceptance

Survivorship of catbird nestlings

The cost of acceptance was the difference in fledgling success in experimentally parasitized and unparasitized nests. An ANOVA was used to test whether the presence of a cowbird nestling, catbird egg removal, and initial brood size affected catbird fledging success. Year did not have a significant effect; therefore, data from 1997 and 1998 were pooled. Only nests that fledged at least one catbird or cowbird chick were included in this analysis. Initial brood size was the number of catbird eggs and chicks that were present on the day that the first catbird chicks hatched minus any nonviable catbird eggs. A catbird egg was nonviable if it did not contain an embryo when cracked open at the end of the nestling stage. Fledging success (F) was calculated as:

$$F = \frac{N}{B - R}$$

where N = number of catbird chicks that fledged, B = initial brood size and R = number of catbird eggs removed. The number of catbird eggs removed was subtracted from the initial brood size in order to determine how catbird egg removal affected the fledging success of the remaining catbird offspring. Fledging success was calculated as a proportion of catbird offspring present on the first day of hatch rather than as a proportion of catbird chicks hatched because some catbird eggs may not have hatched due to the presence of a cowbird chick.

An ANOVA was performed to test whether the day on which the cowbird chick hatched relative to the hatching of the first catbird chicks affected catbird fledging success.

Because of small sample sizes, the days on which the cowbird chicks were

added to nests were divided into two categories: a) one to four days before the catbird chicks hatched, and b) on the same day or after the catbird chicks hatched.

Size and mass of catbird nestlings

An ANOVA with repeated measures (ANOVAR, Potvin et al. 1990, von Ende 1993) was used to test the effect of parasitism, catbird egg removal, and catbird hatching order on the size of catbird chicks on day 1 to day 8. Because tarsus length and mass were highly correlated (Appendix 2), only the statistical tests for tarsus length were presented. The mean brood size over the 8 days was used as a covariate. Year did not have a significant effect; therefore, data collected in 1997 and 1998 were pooled. Only data for nests that had no missing data from day 1 to day 8 were analyzed. Forty nests had missing data on 2 July 1997 because a storm made it impossible to visit catbird nests on that day. Nestlings that hatched on the first day of hatching were designated core chicks (see Forbes et al. 1997). All other nestlings were designated marginal chicks. The experimental unit was the nest; therefore, mean values for core chicks and marginal chicks in a nest were analyzed.

Survivorship and size of cowbird chicks

The fates of cowbirds placed into catbird nests were classified as surviving to day 8 or dying due to predation, starvation, stormy weather, or dipteran larvae infestation. The cowbird was presumably taken by a predator if: 1) the cowbird and some or all of the host nestling(s) were gone or 2) a cowbird of normal mass was gone, but was not the smallest nestling in the nest. The cowbird presumably starved to death if it was the only nestling missing or dead in the nest, and it was underweight relative to cowbird nestlings that fledged from other nests. The cowbird presumably died due to inclement weather when all the nestlings in a nest were found dead in or under the nest or was gone the day after a major storm.

An ANOVA was performed to determine whether the day on which a cowbird was added relative to the hatching of the catbird chicks affected the position of the cowbird nestling within the brood hierarchy. Cowbirds were ranked in terms of mass relative to the catbird chicks in the brood. Cowbirds that were gone before all of the catbirds had hatched were not ranked. A second ANOVA was performed to test the effect of the day on which the cowbird egg was added to the nest and egg removal on whether a cowbird fledged or starved. The days on which the cowbird chicks were added to nests were divided into two categories: a) one to four days before the catbird chicks hatched, and b) on the same day or after the catbird chicks hatched. Fisher's exact tests were used to test whether the day the cowbird chick was added to the nest and catbird egg removal affected whether a cowbird chick fledged or starved. A Fisher's exact test is more appropriate than a chi-squared test when more than 20% of the categories have an expected frequency of less than 5 (Milton 1992:399). An ANOVA was performed to test the effect of the day on which the cowbird chick was added to the nest and catbird egg removal on the size of cowbird chicks on day 8. Because tarsus length and mass are highly correlated (Pearson correlation = 0.87) and resulted in similar findings, only the results for tarsus length were presented.

RESULTS

Outcome of nests

The mean clutch size for 229 catbird nests that survived at least through egg-laying during the three years of the study was 4.4 ± 0.04 eggs (Appendix 3). In 1997 and 1998, 38% of the 242 nests contained chicks that fledged, 52.1% were depredated, 8.7% failed due to storms, and 1.2% were deserted (Table 1). Nest outcome differed

Table 1. Outcome of all Gray Catbird nests found in 1997 and 1998 at Delta Marsh, Manitoba.

	Number of nests (%)				Total nests
	Fledged ¹	Depredated	Storm ²	Deserted	
1997	42 (37.8)	48 (43.2)	20 (18.0)	1 (0.9)	111
1998	50 (38.2)	78 (59.5)	1 (0.8)	2 (1.5)	131
Both years	92 (38.0)	126 (52.1)	21 (8.7)	3 (1.2)	242

¹ In 1997, fledging was defined as surviving to day 8. In 1998, nests were monitored until all nestlings had fledged from the nest (between days 9 and 13). If fledging was defined as surviving to day 8 in 1998, the frequencies would be as follows: Fledged = 44.3%, Depredated = 54.1%, Storm = 0.8%, Deserted = 0.8%.

² Nest destroyed due to storm or nestlings died as a result of exposure to the elements.

significantly in 1997 and 1998 ($\chi^2 = 23.9$, $df = 3$, $P < 0.00005$), with a higher proportion of nests depredated and a lower proportion of nests destroyed by weather in 1998.

Natural parasitism was detected at 3 of 12 catbird nests (25%) monitored daily on or before LD2 to at least LD5 in 1996, 2 of 110 such nests (1.8%) in 1997, and none of 35 such nests in 1998. Frequency of parasitism for all three years was 3.2% ($n = 157$). The stages at which the nests were parasitized and the outcome of the model egg that replaced the real cowbird egg are indicated in Appendix 4.

Egg addition experiments

Conspecific egg additions

All 27 experimentally introduced catbird eggs were accepted regardless of the stage that the nest was parasitized or whether the egg was switched or added. There was no evidence of more than one egg laid in one nest per day in 1997 and 1998 in 95 catbird nests that were found on or before the first catbird egg was laid and survived to at least LD6. No catbird eggs appeared after completion of the normal laying sequence.

Cowbird egg additions

Ejection frequency

Ninety-six percent (with a 95% confidence interval of 91.6 - 99.8%, $n = 94$) of the cowbird eggs experimentally added to catbird nests were ejected. The ejection frequency in this study was almost identical the 94.3% ejection frequency reported by Rothstein (1975a). This was not a statistically significant difference ($Z = 0.37$, $P = 0.36$). All four instances of acceptance in the present study occurred when the cowbird egg was added on LD5. None of the accepted cowbird eggs had peck marks that would have indicated a puncture-ejection attempt (Rothstein 1977). The modal and median

ejection times were within 5 hours of the introduction of the egg model ($n = 90$), with the longest ejection time 2 to 3 days (Figure 1).

Cost of ejection

Only 0.02 ± 0.02 catbird eggs were lost per ejection (2 eggs in 90 ejections). In 1996, two catbird eggs went missing from two nests out of 213 days on which nests were checked during the egg stage, which worked out to a partial predation rate of 0.0093 single eggs per day. When the background level of partial predation rate was considered, the cost of ejection was only 0.01 eggs per ejection or 0.0022 catbird fledglings lost per ejection.

Cost of acceptance

Survivorship of catbird nestlings

The presence of the cowbird chick decreased the proportion of catbird chicks that fledged (Figure 2a), but this difference was not significant ($P = 0.096$, Table 2). The removal of catbird eggs did not affect the fledging success of the remaining catbird eggs (Table 2, Figure 2b). The later the cowbird chick hatched relative to the hatching of the catbirds, the greater the proportion of catbird chicks fledged (Figure 3), but this difference was not significant ($F = 1.29$, $df = 1, 24$, $P = 0.27$, power = 0.19).

Size of catbird nestlings

The catbird core nestlings were significantly larger than marginal nestlings (Table 3, Figure 4). Catbird chicks in nests that received a cowbird chick were smaller than chicks in control nests (Figure 5), but this difference was not significant ($P = 0.12$, Table 3). The removal of a catbird egg did not significantly affect the size of the remaining catbird chicks (Table 3, Figure 6).

Figure 1. Frequency distribution of the ejection time of model Brown-headed Cowbird eggs by Gray Catbirds.

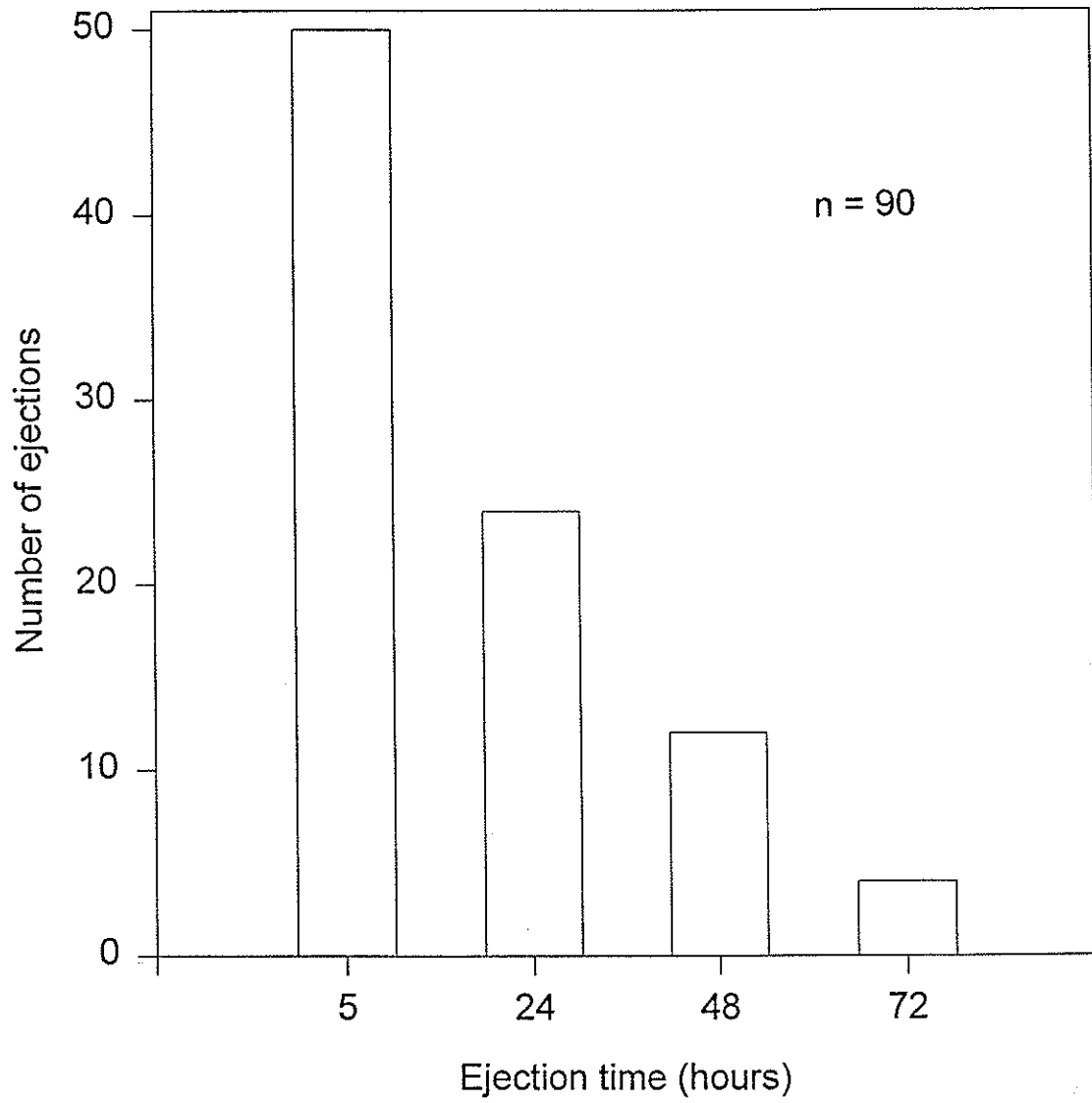


Figure 2. A, the proportion of Gray Catbird brood fledged in parasitized and unparasitized nests. B, the proportion of catbird brood fledged in nests that did and did not have a catbird egg removed. Error bars indicate standard error. Sample sizes are provided on the graph.

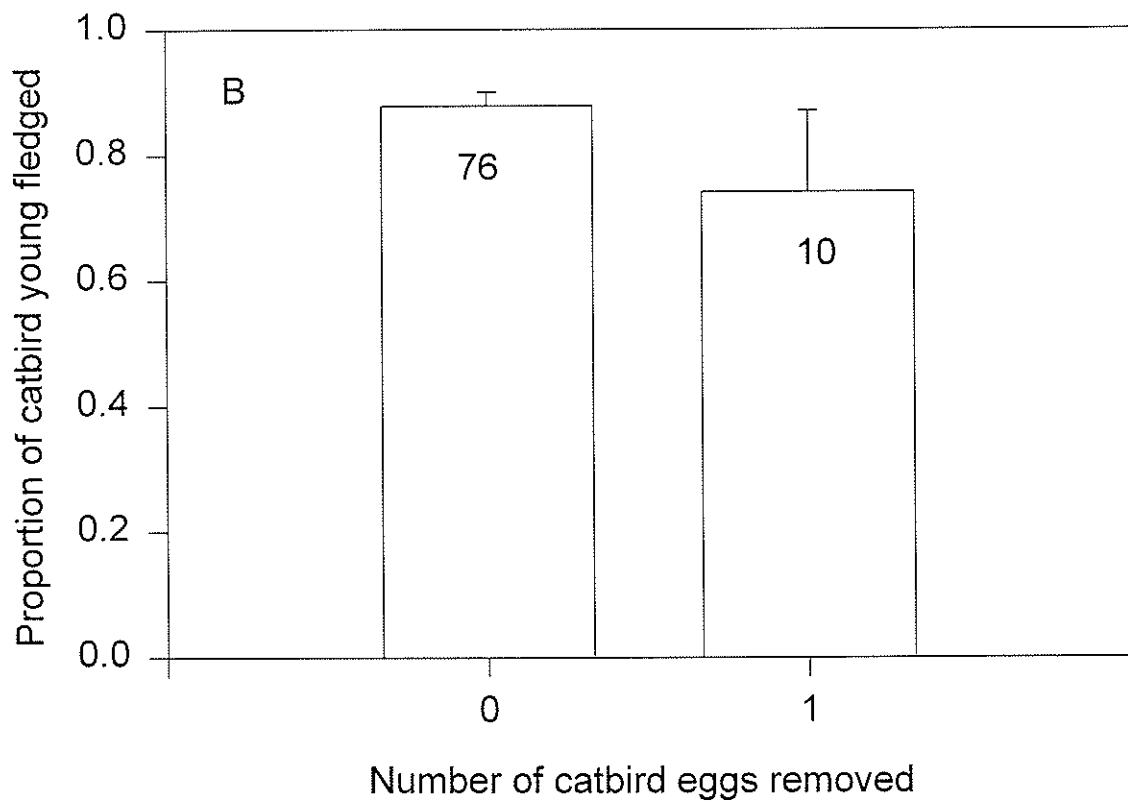
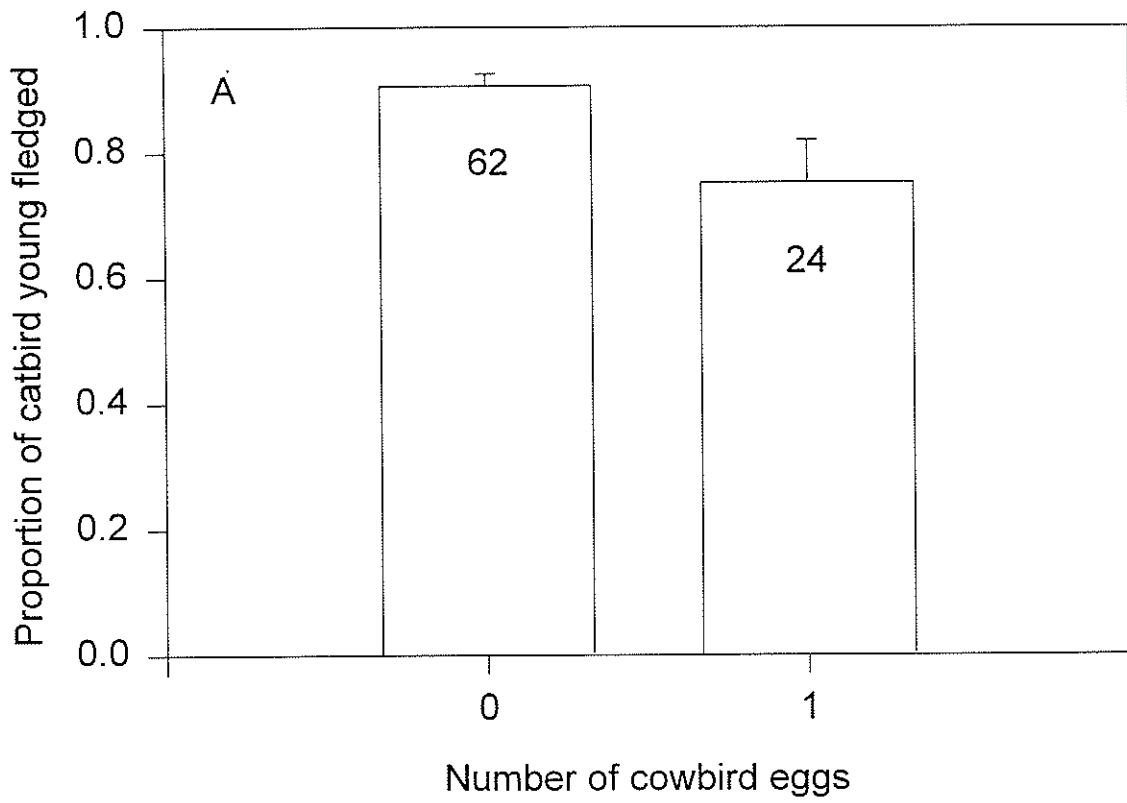


Table 2. The effect of the presence of a Brown-headed Cowbird chick, experimental catbird egg removal and initial brood size on Gray Catbird fledging success.

Effect ¹	F-value	df	P-value		Power
			$\alpha_5 = 0.01$	$\alpha = 0.05$	
Cowbird	5.60	1, 76	0.020	0.096	0.65
Removed	0.008	1, 76	0.93	1.0	0.051
Brood	3.4	3, 76	0.023	0.11	0.74
Cowbird x Brood	0.42	2, 76	0.66	1.0	0.12
Removed x Brood	0.36	1, 76	0.55	0.98	0.091

¹ No values are calculated for interactions involving Cowbird x Removed because unparasitized nests did not have any catbird eggs removed.

Figure 3. The effect of the timing of Brown-headed Cowbird hatching relative to the day on which the first Gray Catbird chicks hatched on the proportion of catbird brood fledged. "Before" - cowbird chick hatched one to four days before the first catbird chicks hatched. "After" - cowbird chick hatched on the same day or one day after the first catbird chicks hatched. Error bars = standard error. Sample sizes are provided on the graph.

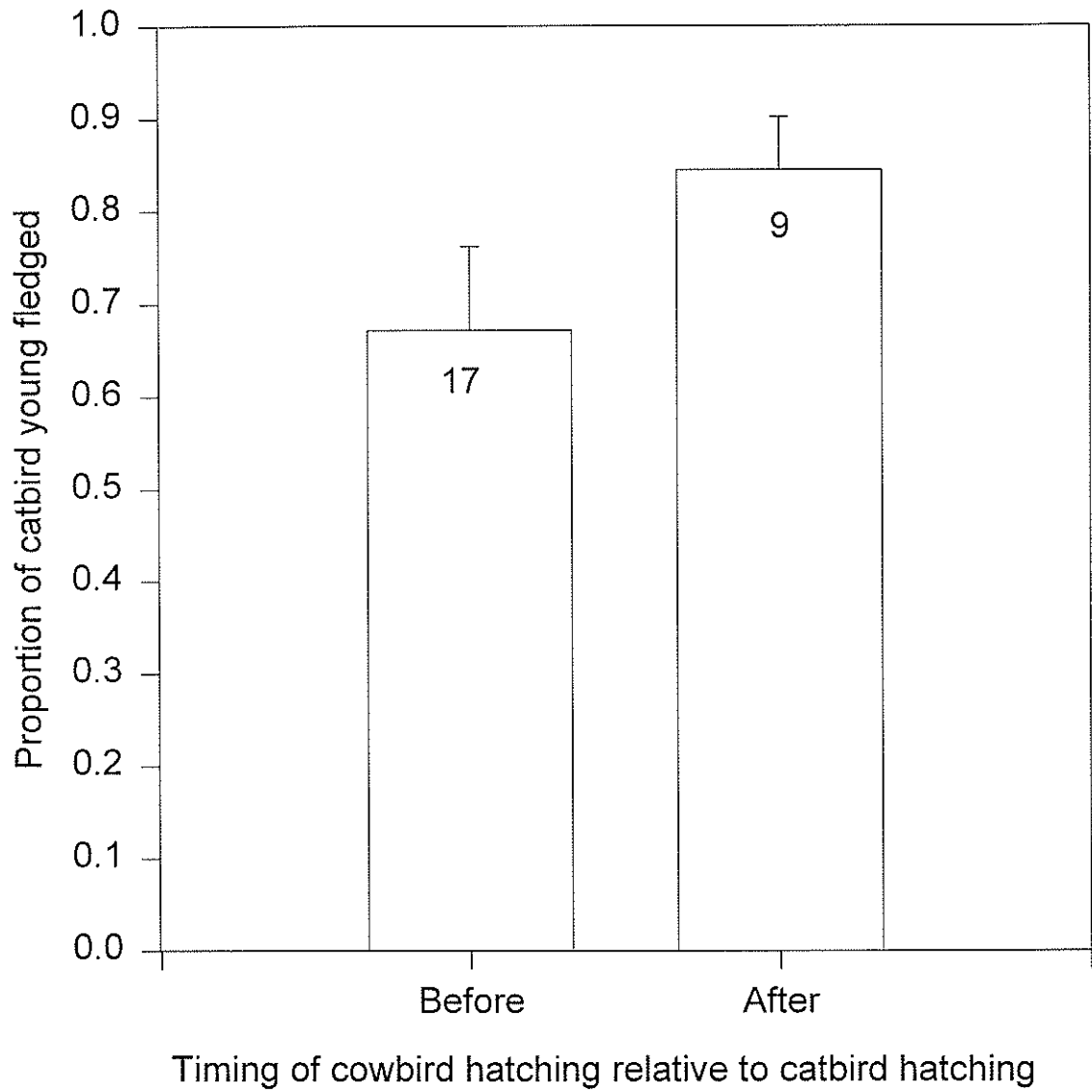
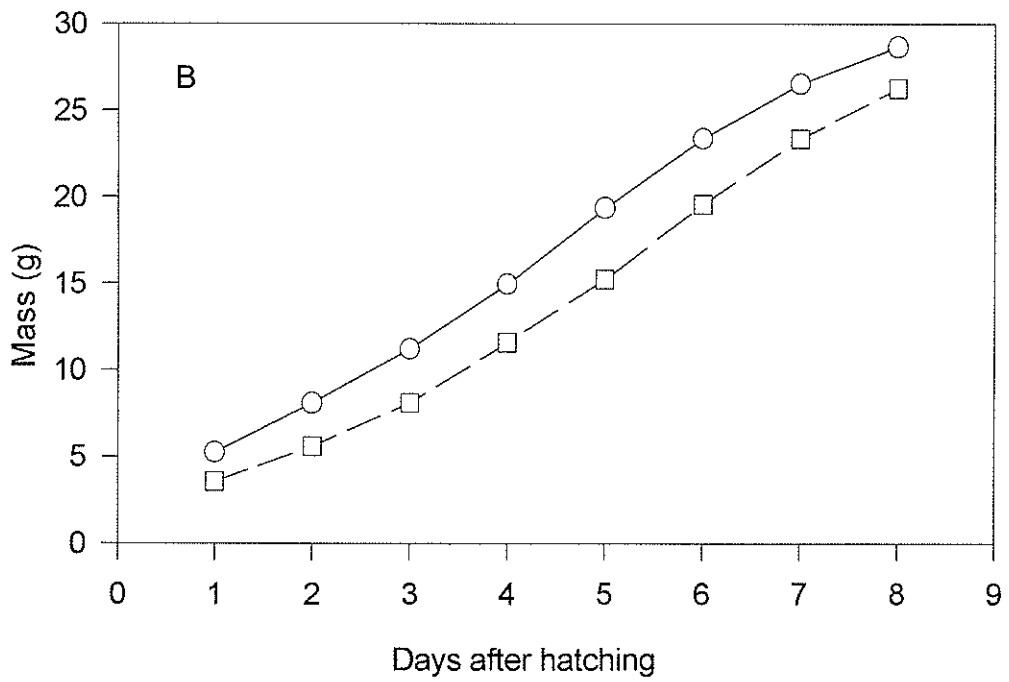
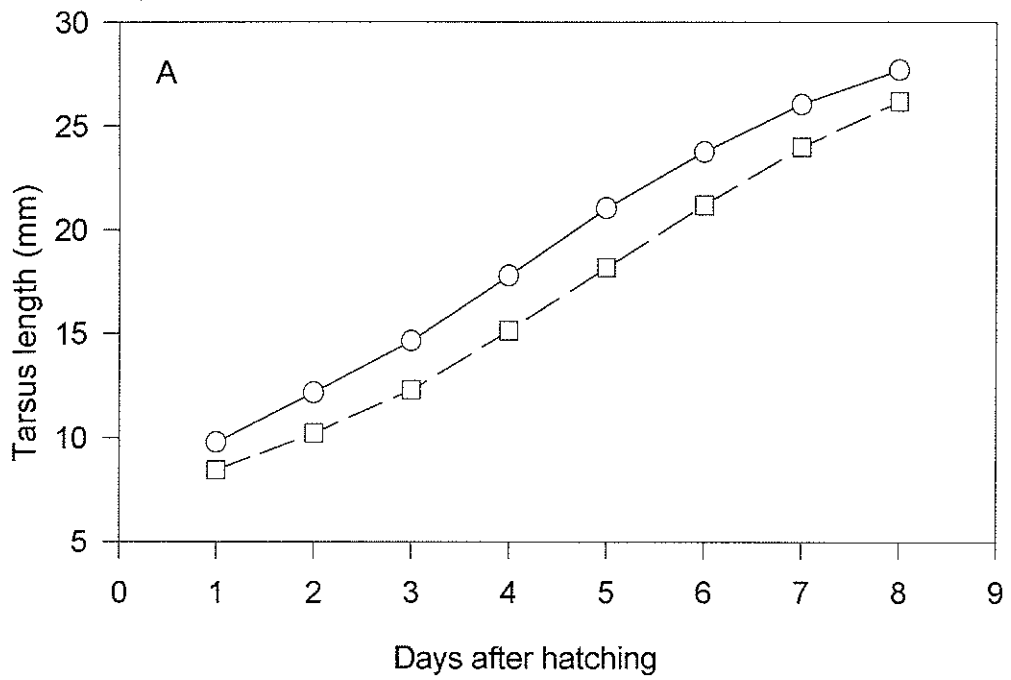


Table 3. The effect of the presence of a Brown-headed Cowbird chick, catbird chick hatching order, and experimental catbird egg removal on the tarsus length of Gray Catbird chicks.

Effect ¹	F-value	df	P-value		Power
			$\alpha_5 = 0.01$	$\alpha = 0.05$	
<i>Covariates</i>					
Brood size	4.01	1, 82	0.048	0.22	0.51
<i>Between subjects</i>					
Cowbird	5.25	1, 82	0.025	0.12	0.62
Core/marginal	41.3	1, 82	< 0.0005	< 0.0025	1.00
Removed	2.97	1, 82	0.089	0.37	0.40
Core/marginal x Cowbird	0.10	1, 82	0.75	1.0	0.06
Core/marginal x Removed	0.07	1, 82	0.79	1.0	0.06

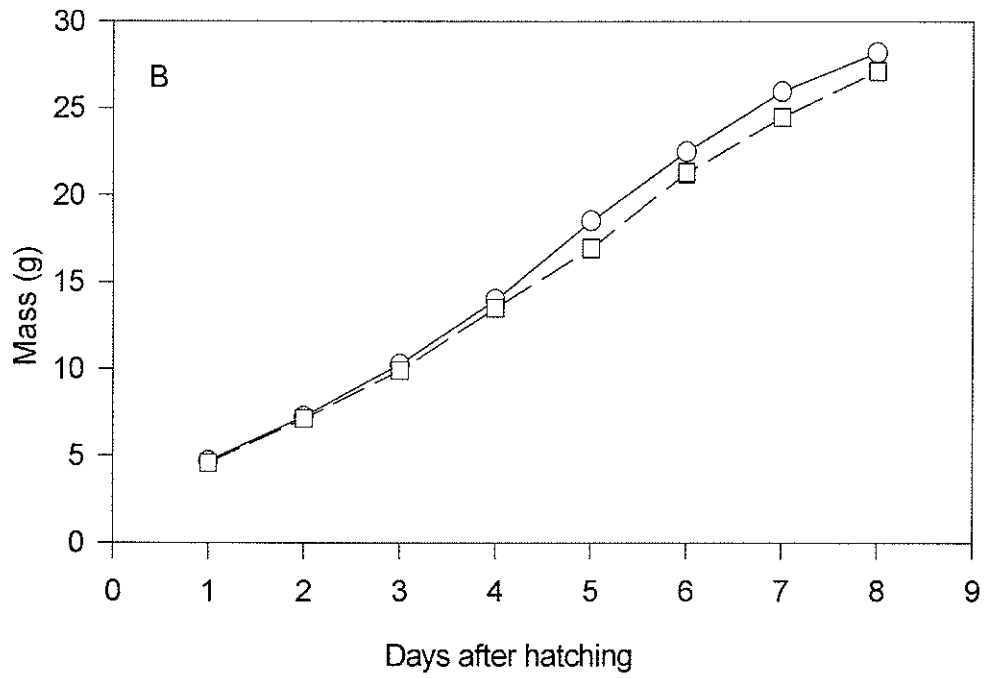
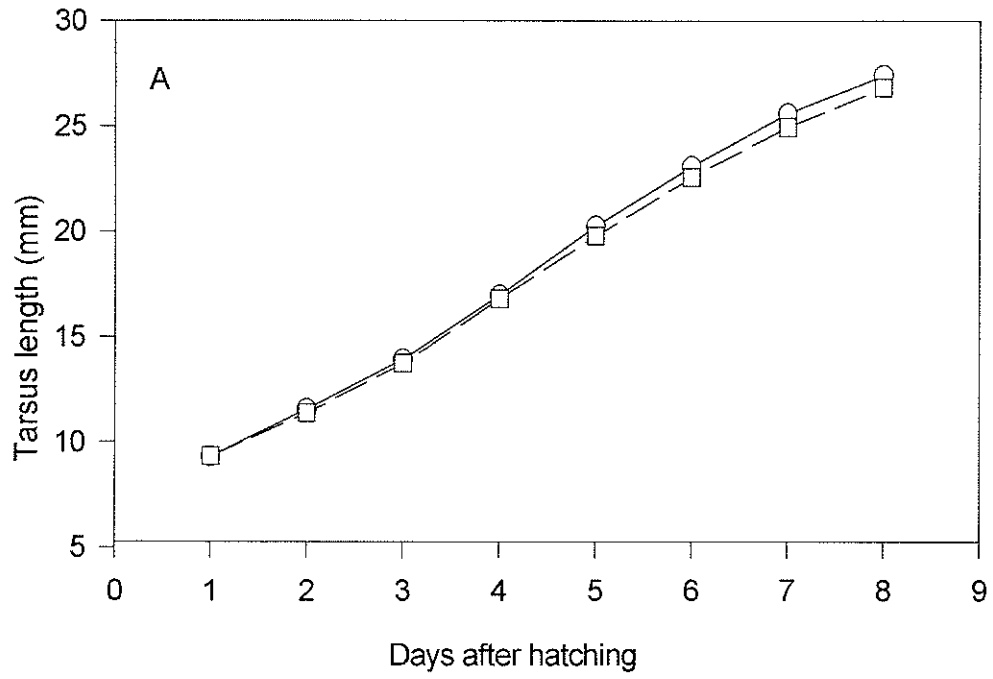
¹ No values are calculated for interactions involving Cowbird x Removed because unparasitized nests did not have any catbird eggs removed.

Figure 4. A, mean tarsus length and, B, mean mass of core and marginal Gray Catbird chicks on days 1 to 8 after hatching. The sample sizes for core and marginal chicks were 59 and 30, respectively. Standard error bars are so small that they are masked by the data point symbols.



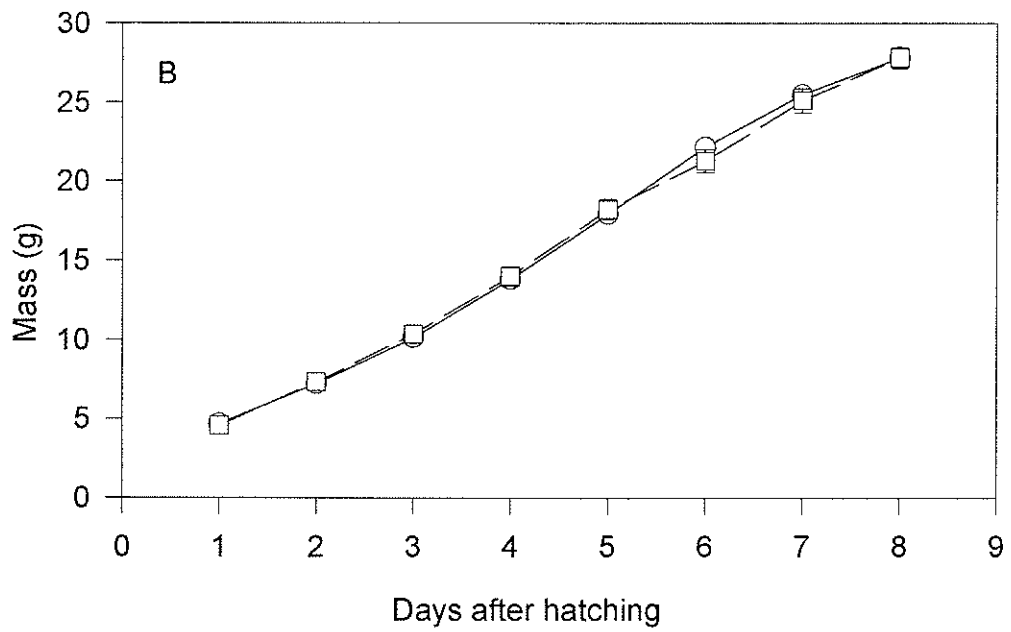
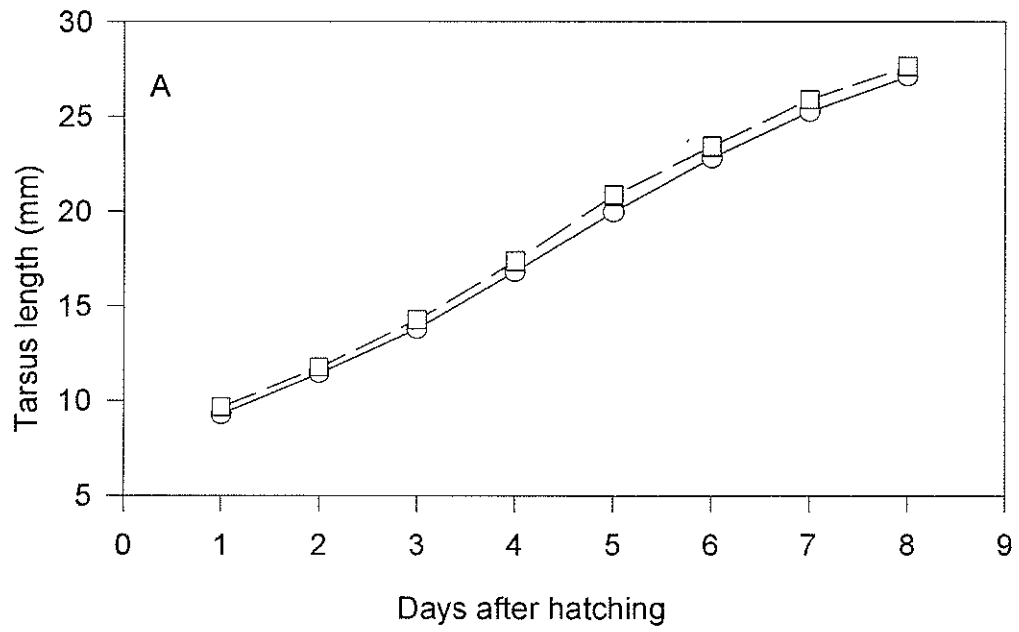
○ Core □ Marginal

Figure 5. A, mean tarsus length and, B, mean mass of Gray Catbird chicks on days 1 to 8 after hatching in nests that experimentally received a cowbird chick (parasitized, n = 57) and control nests (unparasitized, n = 32). Standard error bars are so small that they are masked by the data point symbols.



□ Parasitized ○ Unparasitized

Figure 6. A, mean tarsus length and, B, mean mass of Gray Catbird chicks on days 1 to 8 after hatching in experimentally parasitized nests that did ($n = 79$) and did not ($n = 10$) have a catbird egg experimentally removed at the time that the cowbird chick was added to the nest. Standard error bars are so small that they are masked by the data point symbols.



- Parasitized, with no catbird egg removed
- Parasitized, with catbird egg removed

Survivorship and size of cowbird chicks

Overall, 34% of the cowbird chicks fledged; the remaining cowbird chicks died of various causes (Table 4). The day on which the cowbird chick hatched relative to the day on which the catbird chicks hatched had a significant effect on the size of the cowbird chick relative to the catbird chicks ($F = 5.77$, $df = 5, 26$, $P = 0.001$). The later the cowbird chick hatched relative to the catbird chicks, the lower it was in the mass hierarchy. When a cowbird chick hatched three to four days before the catbird chicks, it became the largest chick in the brood, but when a cowbird hatched the day after the first catbirds hatched, the cowbird was the smallest nestling in the brood (Figure 7). 85.7% of the cowbird chicks fledged when the cowbird chick hatched before any of the catbird chicks hatched ($n = 12$), whereas only 50% of the cowbird chicks fledged when the cowbird chick hatched on the same day or after the first catbird chicks hatched ($n = 6$). This difference was not significant (Fisher's exact test, $P = 0.13$). Sixty-seven percent of the cowbird chicks fledged when no catbird eggs were removed, whereas 82% of the cowbird chicks fledged when a catbird egg was removed. Neither the removal of a catbird egg ($F = 0.013$, $df = 1, 13$, $P = 0.91$) nor the day on which the cowbird chick hatched relative to the catbird chicks ($F = 1.13$, $df = 1, 13$, $P = 0.30$) significantly affected the size of cowbird chicks on day 8 (Figure 8).

Does the cost of acceptance exceed the cost of ejection?

Of catbird young present on the day of first hatch, the mean (\pm standard error) proportion that fledged in unparasitized and parasitized nests was 0.91 (± 0.02) and 0.75 (± 0.07), respectively (Table 2, Figure 2). Therefore, the presence of the cowbird chick decreased the proportion of catbird young that fledged by an average of 16%. Because the mean initial brood size was 3.95 ± 0.10 ($n = 88$), the presence of a cowbird chick

Table 4. Fate of Brown-headed Cowbird chicks placed into Gray Catbird nests.

Year	Number (%)					Total
	Fledged	Starved	Depredated	Died during storm	Died due to larval infestation	
1997	2 (15)	3 (23)	4 (31)	4 (31)	0	13
1998	13 (42)	8 (26)	8 (26)	1 (3)	1 (3)	31
Total	15 (34)	11 (25)	12 (27)	5 (11)	1 (2)	44

Figure 7. The effect of the day on which the Brown-headed Cowbird hatched relative to the hatching of the first Gray Catbird chicks on the cowbird mass ranking relative to the mass of the catbirds. If ranked 1, the cowbird was the largest chick in the brood. Sample sizes are provided on the graph. Error bars = standard error.

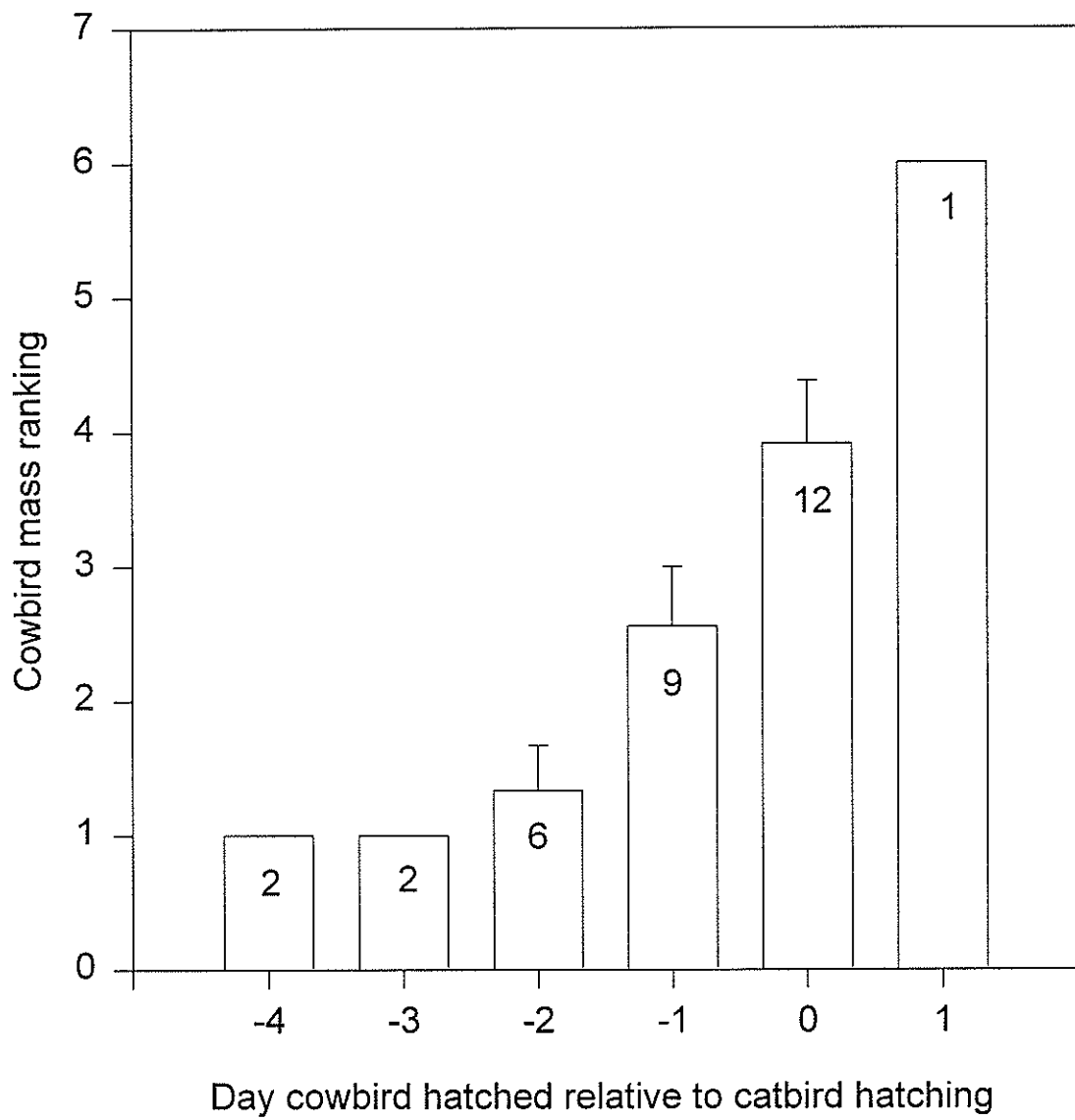
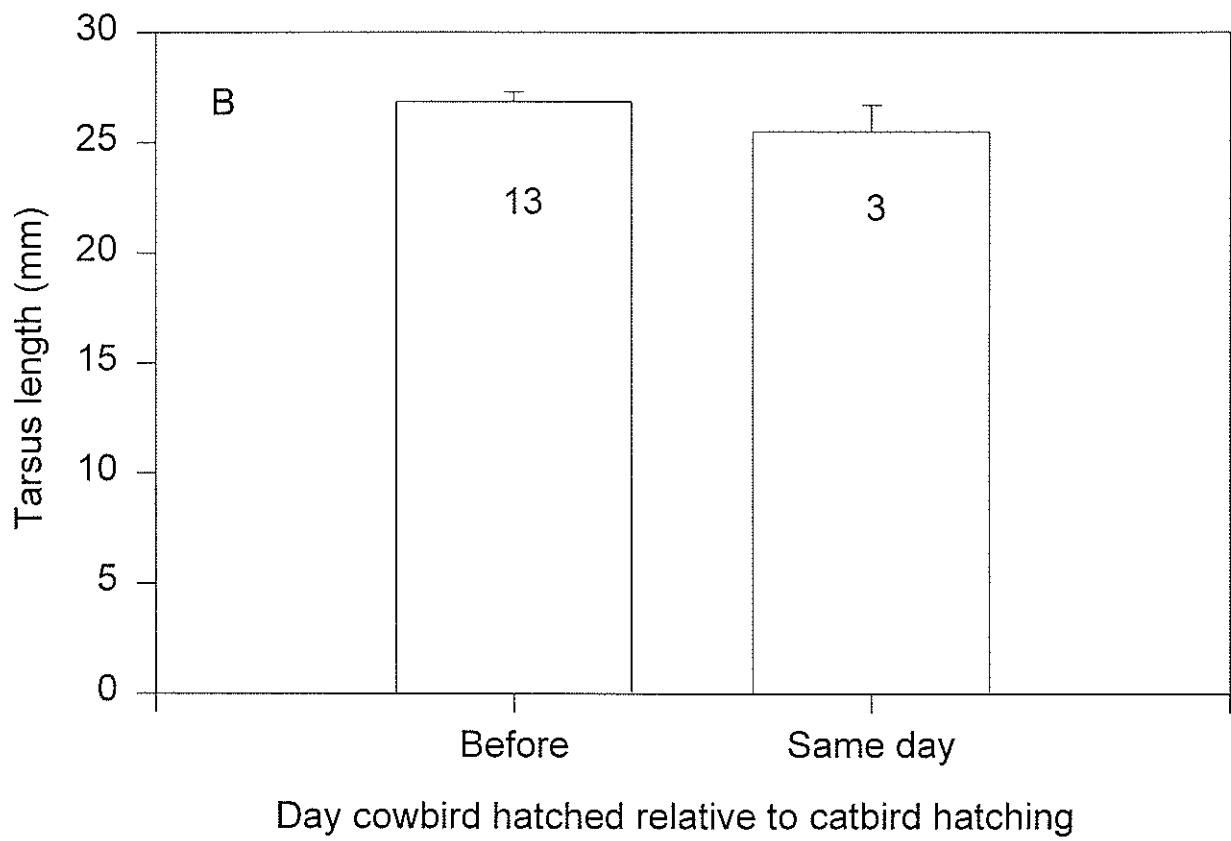
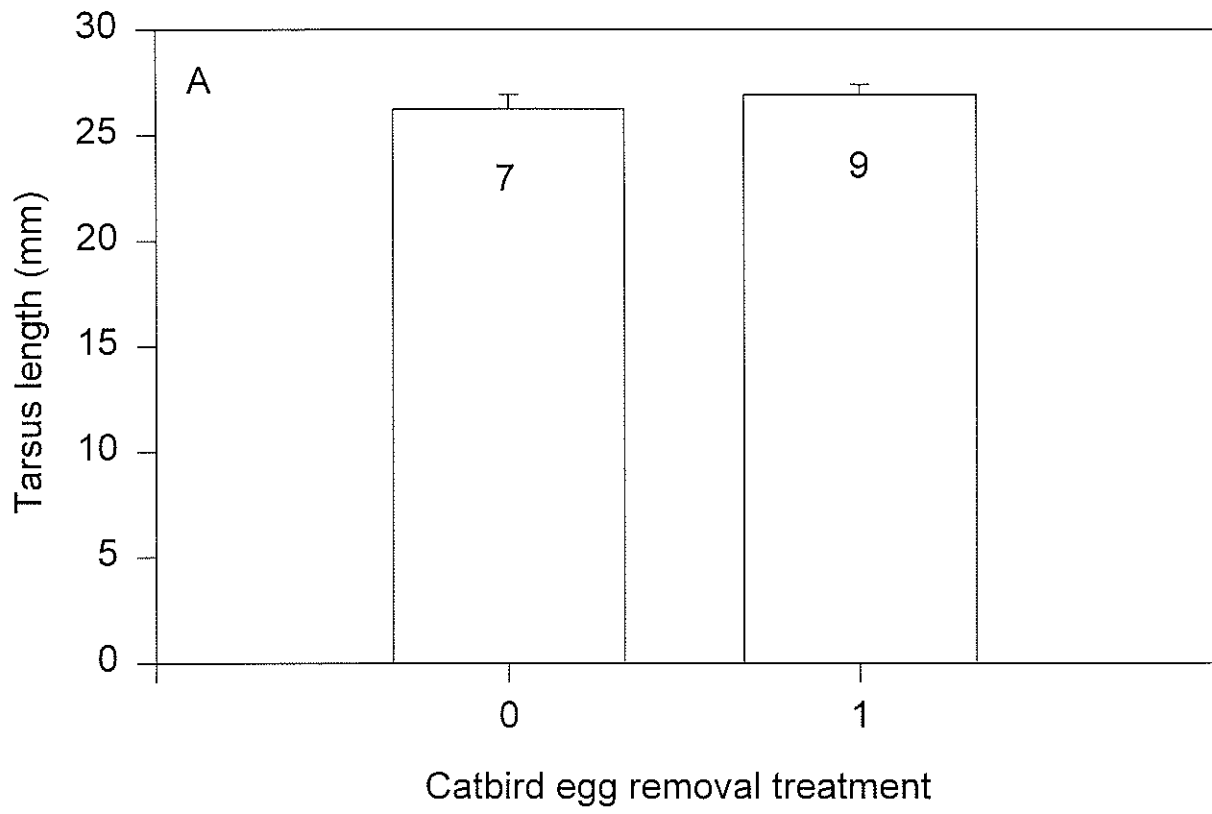


Figure 8. A, the effect of experimental Gray Catbird egg removal on the mean tarsus length of Brown-headed Cowbird chicks. B, the effect of the day on which cowbird hatched relative to catbird hatching on tarsus length of cowbird chicks. "Before" - cowbird chick hatched one to four days before the first catbird chicks hatched. "Same day" - cowbird chick hatched on the same day as the first catbird chicks. Sample sizes are provided on the graph. Error bars = standard error.



resulted in a mean of 0.63 fewer chicks to fledge. The cost of ejection was 0.0022 catbird fledglings per nest, which is much less than the cost of accepting a cowbird chick.

DISCUSSION

Two possible selective pressures for egg ejection in Gray Catbirds are brood parasitism by catbirds and by Brown-headed Cowbirds. The lack of evidence for conspecific brood parasitism and the acceptance of conspecific eggs do not support the hypothesis that egg ejection in Gray Catbirds evolved in response to conspecific brood parasitism. Rothstein (1982a) found that catbirds accepted five model eggs simulating catbird eggs, even though the paint used for the ground colour was darker than real catbird eggs. Acceptance of conspecific eggs during egg laying has been found in at least six other rejecter species: Mourning Doves (*Zenaida macroura*), Eastern Kingbird (*Tyrannus tyrannus*), Brown Thrasher, American Robin (*Turdus migratorius*), Yellow Warbler (*Dendroica petechia*) and Great-tailed Grackle (*Quiscalus mexicanus*) (Table 5). The Gray Catbird is not unique in conspecific brood parasitism not being the selective pressure for egg ejection.

The costs of ejection were almost negligible; only 0.01 catbird eggs (or 0.0022 catbird fledglings) were lost per ejection. When background rates of partial predation are taken into account, the cost of ejection is only 0.01 catbird eggs per ejection (or 0.0022 catbird fledglings). The cost of ejection, in terms of host eggs, for catbirds was similar to that recorded for other grasp-ejecters (Table 6). Grasp-ejection generally is less costly than puncture-ejection. Puncture-ejecters have smaller bills and first puncture or break the cowbird egg and carry it away (Røskoft et al. 1993, Sealy 1996). Because cowbird eggs have thicker eggshells than expected for their size, relative to other icterines (Spaw and Rohwer 1987, Rahn et al. 1988, Picman 1989), puncture-

Table 5. Percentage of real conspecific eggs ejected by rejecter species during the egg-laying stage.

Species	Percent conspecific eggs ejected (no. nests)			Reference
	Added	Switched	Total	
Mourning Dove	0 (14)	-	0 (14)	Peer and Bollinger 1998
Eastern Kingbird	17 (6)	-	17 (6)	Bischoff and Murphy 1993
	9 (11)	-	9 (11)	Gifford 1993
	0 (11) ¹	-	0 (11)	Sealy and Bazin 1995
Brown Thrasher	0 (9)	-	0 (9)	Haas and Haas 1998
Gray Catbird	0 (10)	0 (17)	0 (27)	This study
American Robin	0 (10)	-	0 (10)	Briskie et al. 1992
Yellow Warbler	0 (53) ²	0 (11)	0 (64)	Sealy et al. 1989
Great-tailed Grackle	-	6.7 (15) ³	6.7 (15)	Lanier 1982
			8.1 (246) ⁴	Peer 1998

¹ This does not include conspecific eggs introduced into empty nests; 30% of 20 such eggs were ejected.

² Sixteen additional yellow warbler eggs added to unlined nests were buried because of continued nest-building behavior.

³ Two other conspecific eggs disappeared, but Lanier (1982) suggested that their disappearance may have been for reasons other than an anti-parasitic response.

⁴ Conspecific Great-tailed Grackle eggs were both added to grackle nests and switched with single grackle eggs, but the breakdown of sample sizes for each treatment were not indicated.

Table 6. The cost of ejection for puncture- and grasp-ejecters of Brown-headed Cowbird eggs.

Host species ¹	No. host eggs		Reference
	lost per ejection	No. ejections	
<u>Puncture-ejecters</u>			
Warbling Vireo	0.10	29	Sealy 1996, unpubl. data
Baltimore Oriole	0.38	16	Sealy and Neudorf 1995
Bullock's Oriole	0.26	34	Rohwer et al. 1989, Røskaft et al. 1993
<u>Grasp-ejecters</u>			
Eastern Kingbird	0.07	88	Sealy and Bazin 1995
Western Kingbird	0	7	Rohwer et al. 1989
American Robin	0	2	Rohwer et al. 1989
	0.08	59	Sealy, unpubl. data
Gray Catbird	0.01	92	This study
Sage Thrasher	0.18	11	Rich and Rothstein 1985

¹ Scientific names of species not mentioned in text: Baltimore Oriole, *Icterus galbula*; Western Kingbird, *Tyrannus verticalis*.

ejecters sometimes damage their own eggs while attempting to puncture-eject the cowbird egg (Rohwer et al. 1989). Catbirds have been observed both grasp-ejecting (e.g. A. Wilson in Brewer 1840:371, Berger 1951) and puncture-ejecting cowbird eggs (J.V. Briskie, pers. comm). Evidence that they normally grasp-eject foreign eggs is their ability to eject model eggs made of plaster-of-Paris (e.g. Rothstein 1975a, 1982a; this study). Model cowbird eggs placed in the nests of puncture-ejecters are often left in the nest heavily pecked (Rothstein 1976, 1977).

Even though parasitism did not have a significant effect on the fledging success of catbird chicks, this does not necessarily mean that the effect of parasitism is not biologically significant. Statistical significance should not be confused with biological significance (Krebs 1989:8). I argue that because the recoverable cost of parasitism (0.63 catbird fledglings per nest) was more than 250 times greater than the cost of ejection (0.0022 catbird fledglings per nest), it is adaptive for catbirds to eject cowbird eggs. Therefore, the hypothesis that cowbird parasitism is a current selective pressure maintaining egg ejection in catbirds was supported. Røskaft et al. (1993) used this same argument when they found that Bullock's Orioles did not incur a significant cost of parasitism because the cost of rearing a cowbird chick when the brood size was four (0.4 oriole fledglings) exceeded the cost of ejection (0.26 oriole eggs). Their argument would have been even stronger had they converted the cost of ejection into the same units as the cost of parasitism.

The calculation of the recoverable cost of parasitism for catbirds did not include differential post-fledging survivorship of catbird chicks in parasitized and unparasitized nests. In studies of many other bird species, smaller nestlings suffered a higher rate of post-fledging mortality than larger ones (e.g., Perrins 1965, Dhont 1979, Martin 1987, Magrath 1991, Husby and Slagvold 1992, Lindén et al. 1992, but see Smith 1981). Catbird chicks that fledged in parasitized nests were smaller than those that fledged

from unparasitized nests, but this difference was not significant (Figure 5). Some researchers have found that host nestlings raised in parasitized nests of other species were smaller than nestlings in unparasitized nests (e.g., Smith 1981, Marvil and Cruz 1989, Soler and Soler 1991, Dearborn et al. 1998). Others have found no effect (e.g., Wolf 1987, Weatherhead 1989, Ortega 1991, Petit 1991, Smith and Arcese 1994, Eckerle and Breitwisch 1997, Clotfelter and Yasukawa 1999). Smith's (1981) study is the only one to compare post-fledgling survivorship of host young raised in parasitized and unparasitized nests. Interestingly, he found that although Song Sparrows weighed less in parasitized nests, they did not have a lower probability of surviving to independence than sparrows raised in unparasitized nests.

Host egg removal and the timing of cowbird hatching relative to the hatching of the catbird chicks are two factors that are under the control of the female cowbird that may affect the cost of parasitism for catbirds. This study provided the first experimental test of the hypothesis that host egg removal reduces nestling competition. The removal of a catbird egg did not significantly affect the probability that cowbird chicks will fledge, nor did it affect the fledging success of the remaining catbird eggs (Figure 2). Therefore, I did not find support for the hypothesis that increasing the nonrecoverable costs of parasitism (i.e., host egg removal) decreases the recoverable costs of parasitism (i.e., host fledging success), however, the power of this test was only 5%. My findings contrast with Weatherhead (1989) who found that parasitized Red-winged Blackbird young compensated for the initial cost imposed by clutch reduction that resulted from host egg removal. The remaining eggs in naturally parasitized blackbird nests had a greater probability of fledging than eggs in unparasitized nests.

There are many other hypotheses for the function of host egg removal by the female cowbird (reviewed in Sealy 1992). Sealy (1992) did not find that Yellow Warblers were more likely to accept parasitized clutches from which a warbler egg was removed.

Experimental support for the incubation limit hypothesis was also not found because egg removal did not reduce incubation lengths or increase hatchability of parasitic eggs (McMaster and Sealy 1997, Wood and Bollinger 1997, but see Peer and Bollinger, in press). Therefore, there is no convincing empirical evidence for the adaptive function of host egg removal.

Cowbirds have evolved a shorter incubation period than expected for their egg size (Briskie and Sealy 1990, McMaster and Sealy 1998). This may be particularly important for successful parasitism of large hosts, such as the catbird. The earlier the cowbird chick hatched in the present study, the higher the cowbird was in the nestling hierarchy (Figure 7). Cowbirds that hatched after catbird chicks became one of the smallest nestlings in the brood. This did not translate into a significant effect on the survivorship of cowbird or catbird chicks, although the earlier the cowbird hatched, the more likely it was to fledge, and the lower the catbird fledging success (Figure 3). By hatching before host young, cowbird nestlings become one of the largest nestlings in the brood (Figure 7). As demonstrated in Chapter 3, being the largest nestling in the brood is advantageous because adult catbirds preferentially feed nestlings that reach the highest. Being larger than the host chicks enables cowbird chicks to increase their competitive ability, divert parental care away from host nestmates, and increase their probability of survival.

Ten of 34 mimid species that are recognized by Monroe and Sibley (1993) have been tested for ejection behaviour through experimental parasitism. Seven are ejecters, two are accepters, and one shows intermediate responses (Table 7). A phylogenetic analysis of egg ejection behaviour in the family Mimidae is a critical study to determine whether egg ejection evolved in Gray Catbirds, rather than in an ancestor.

Unfortunately, a phylogenetic analysis for the Mimidae has not been done, therefore, it is impossible to discern the pattern of evolution of egg ejection. Fossil evidence for both

Table 7. Mimid species tested for rejection behaviour with real or artificial eggs.

Species ¹	Location	Frequency of observed parasitism, % (n) ²	Parasitic egg ³	Frequency of rejection, % ⁴	No. nests tested	Reference
<u>Accepters</u>						
California Thrasher	California	-	BHCB	accepter ⁵	-	Rich and Rothstein 1985
Le Conte's Thrasher	N/A	-	BHCB	accepter ⁵	-	Rich and Rothstein 1985
<u>Intermediate</u>						
Northern Mockingbird	Connecticut ⁶	-	BHCB	25.0	4	Rothstein 1975a
	Texas	0 (48)	BHCB	≈50	≈ 20	Mason (pers. comm. in Friedmann and Kiff 1985)

Ejecters

Gray Catbird	Connecticut ⁶	-	BHCB	94.3	53	Rothstein 1975a
	Manitoba	1.4 (145)	BHCB	95.7	94	This study
Chalk-browed Mockingbird	Argentina	78.1 (65)	SHCB	17.6	17	Fraga 1985
			(s)			
	Argentina	78.1 (65)	SHCB	100	10	Fraga 1985
			(i)			
Sage Thrasher	Idaho	0 (40)	BHCB	100	11	Rich and Rothstein 1985
Brown Thrasher	Connecticut ⁶	-	BHCB	96.3	26	Rothstein 1975a
	North Dakota	12 (136)	BHCB	57.8	64	Haas and Haas 1998
Curve-billed Thrasher	Texas	96 (26)	BRCB	100	4	Carter 1986
Crissal Thrasher	Arizona	0 (15)	BHCB	100	9	Finch 1982
Pearly-eyed Thrasher	Puerto Rico	0 (17)	SHCB	81	17	Cruz et al. 1989

¹ Scientific names of species not mentioned in text: California Thrasher, *T. redivivum*; Le Conte's Thrasher, *T. lecontei*; Northern Mockingbird *M. polyglottus*; Sage Thrasher, *Oreoscoptes montanus*; Curve-billed Thrasher, *T. curvirostre*; Crissal Thrasher, *T. dorsale*; Pearly-eyed Thrasher, *Margarops fuscatus*.

² The actual parasitism frequency for ejecter species may be much higher than the apparent rejection frequency if the parasitic egg is often ejected before it is detected by the researcher (Rothstein 1977, Sealy and Bazin 1995). U = unknown.³ BHCB = Brown-headed Cowbird, BRCB = Bronzed Cowbird, SHCB (s) = spotted Shiny Cowbird egg, SHCB (i) = immaculate Shiny Cowbird egg.

⁴ Rejection frequency was by ejection in all species except for the Sage Thrasher, in which 91% was by ejection and 9% was by nest desertion.

⁵ Rothstein (pers. obs. in Rich and Rothstein 1985) reported Le Conte's Thrasher and California Thrashers as accepter species.

⁶ Rothstein (1975a) conducted his study in Connecticut, Manitoba, Nebraska, Michigan, and Maryland.

the catbird and cowbird dates back to the late Pleistocene (< 400 000 years before present) (Parmalee 1992, Lowther 1993). In the present study, I have identified the current selective pressures for egg ejection in Gray Catbirds. However, it cannot be used to determine the selective pressures that were necessary in the evolution of egg ejection in Gray Catbirds unless there is evidence that egg ejection evolved after the Gray Catbird split from its ancestor.

Why is ejection behaviour not more common?

As egg ejection appears to be so beneficial, why is it not more common among species that are parasitized by cowbirds? There are two main hypotheses for the lack of egg ejection behaviour: evolutionary lag and evolutionary equilibrium. According to the evolutionary lag hypothesis, all birds under selection pressure to evolve ejection behaviour will eventually evolve it (Rothstein 1975a). The evolutionary lag hypothesis is untestable, but tends to be the default hypothesis when the evolutionary equilibrium hypothesis is not supported (e.g. Sealy 1996, Kattan 1998). According to the evolutionary equilibrium hypothesis, hosts accept cowbird eggs because they are either physically constrained from removing them, or because the costs of ejection outweigh the costs of acceptance (Rohwer and Spaw 1988). Birds with small bills may not be able to grasp cowbird eggs and, therefore, must puncture the eggs to eject them. The probability of hosts breaking at least one of their own eggs is increased if their bill ricochets off the cowbird's egg and strikes their own. Puncture-ejecters, therefore, incur a higher cost of ejection than grasp-ejecters (Table 6), and there may be a bill size below which it is too costly for a species to puncture-eject cowbird eggs.

Support for the evolutionary equilibrium hypothesis was provided by Rohwer and Spaw's (1988) survey of bill sizes. They found that accepters and puncture-ejecters generally had smaller bills than grasp-ejecters. Sealy's (1996) discovery of a small

puncture ejecter, the Warbling Vireo (15 g), casts some doubt on the evolutionary equilibrium hypothesis because this species incurred no greater cost of ejection than did a larger puncture-ejecter, the Baltimore Oriole (33 g). The existence of such a small host puncture-ejecting cowbird eggs weakens the hypothesis that hosts with bills larger than the Warbling Vireo's are constrained in ejecting cowbird eggs.

With respect to the evolutionary equilibrium hypothesis, it is often believed that the cost of ejection is too high for ejection to evolve, but I suggest that for some species, the cost of parasitism is not as high as traditionally believed. As described above, the cost of parasitism is of two types. Non-recoverable costs, such as host egg removal, will be incurred regardless of whether the cowbird egg is ejected. Recoverable costs, such as brood reduction and nestling competition, are not incurred when the cowbird egg is ejected. Recoverable and non-recoverable costs seldom have been discussed, with the exception of a few studies (Røskaft et al. 1990, Smith and Arcese 1994, Ward et al. 1996, Lotem and Nakamura 1998). It should be emphasized that egg ejection is not expected to evolve if the cost of ejection is greater than the recoverable cost of parasitism. Parasitism is often cited as being costly, but when the cost of parasitism is presented in the literature, it is always presented as the total cost of parasitism. Payne (1997) stated that the greatest effect of cowbird parasitism occurs in the form of egg removal. The recoverable costs of parasitism for large hosts, such as Northern Cardinals (*Cardinalis cardinalis*), Red-winged Blackbirds (*Agelaius phoeniceus*), and Wood Thrushes (*Hylocichla mustelina*) may be negligible and, hence, egg ejection is not selected (e.g., Ortega and Cruz 1988, Weatherhead 1989, Donovan et al. 1995, Eckerle and Breitwisch 1997). Admittedly, researchers are having a difficult enough time accurately estimating the total cost of parasitism (see Pease and Grzybowski 1995; Lorenzana and Sealy, in press), without subdividing the cost of parasitism into its two components. Nonetheless, researchers should be aware of the distinction between the

two types of costs of parasitism and their roles in the evolution of antiparasite responses, such as egg ejection.

In summary, catbirds did not eject foreign conspecific eggs, and no evidence of conspecific brood parasitism was detected; therefore, there is no evidence to suggest that conspecific brood parasitism was an important selective pressure in the evolution of egg ejection. A significant cost of accepting cowbird eggs was not detected in terms of either catbird fledgling success or mass. Nonetheless, I conclude that cowbird parasitism selects for egg ejection because the cost of acceptance is more than 100 times greater than the cost of ejection, and this difference is biologically significant. However, without knowing the pattern of egg ejection evolution in the Mimidae family, I am unable to conclude that cowbird parasitism was an important selective pressure in the evolution of Gray Catbirds.

Chapter 2. Effect of cowbird parasitism on catbird provisioning

The cost of parasitism in terms of a host's current breeding attempt has been calculated in many studies (e.g., Smith 1981, Weatherhead 1989, Petit 1991, reviewed in Lorenzana and Sealy, in press). It is much more difficult to measure whether parasitized adults incur a future cost of parasitism. It has been suggested that parasitized adults suffer decreased survival and/or lifetime reproductive success because they work harder to feed parasitized broods (e.g., Furrer *in* Friedmann et al. 1977, May and Robinson 1985, Dearborn et al. 1998). Only one study has compared the survival and reproductive success of adults that cared for parasitized and unparasitized broods in the previous year (Payne and Payne 1998). In the present study, I used an indirect method of comparing the amount of provisioning at parasitized and unparasitized nests of the Gray Catbird as a means of assessing the long-term cost of parasitism (see Dearborn et al. 1998). Life history theory predicts that increases in nest provisioning will decrease adult survival and/or reduce future reproductive success by decreasing energy available for investment in subsequent broods (Stearns 1992). It has been found in many empirical studies that birds rearing larger broods experience decreased survival and/or future reproductive success (reviewed in Nur 1988:165), presumably because they work harder to care for larger broods.

One prediction of the hypothesis that catbirds experience a future cost of parasitism is that catbirds increase their parental effort when caring for parasitized broods. The second prediction is that parasitized catbirds have reduced survivorship and fecundity in years subsequent to being parasitized due to increased parental effort. Only the first prediction of the hypothesis was tested in this study. The level of parental care was measured at each catbird nest in terms of four parameters: feeding rate, visitation rate, food load, and amount of time spent at the nest. In catbirds, both sexes

feed the young (Gabrielson 1913, Zimmerman 1963, Johnson and Best 1982), therefore, each of these parameters was measured separately for males and females to determine whether there were differences in caring for parasitized and unparasitized nests for one sex, but not the other. It was necessary to quantify both visitation and feeding rates because birds returning to the nest did not always bring food with them. An increase in visitation rates at parasitized nests may increase the risk of predation by making a nest more obvious to predators. The volume of food brought with each visit was measured as a crude estimate of the amount of work that was being done during each feeding trip. It should generally require more energy for catbirds to capture larger prey items because they are generally faster and more difficult to handle than small prey items (e.g., dragonflies versus slower moving chironomids), or multiple small prey items as opposed to single small prey items. In several species, provisioning rate is negatively correlated with prey size (Royama 1966, Tinbergen 1981, Lifjeld 1988). The amount of time spent at the nest was quantified to see whether there was a trade-off between visitation and the amount of time spent at the nest. Dearborn et al. (1998) suggested that increased energy spent on thermoregulation by the host chicks due to decreased parental brooding may contribute to low growth rates in parasitized nests, but they did not find any evidence for this.

METHODS

Data collection

This project was conducted from mid-May to early July 1998 at Delta Marsh, Manitoba. See General Introduction for more details about the study site. Newly hatched cowbird chicks were placed into catbird nests generally one to two days before the catbird chicks hatched to mimic the time that naturally laid cowbirds would hatch in catbird nests. See Chapter 1 for details about how cowbird chicks were obtained. All 58

nests that survived to day 4 or 5 after the first catbird chicks hatched were videotaped for one hour between 0830 and 2130 h. Two nests were videotaped 3 days post-hatch, 37 nests on day 4, and 19 nests on day 5. Nests were videotaped using a Sony CCD-TR3000 Hi 8 recorder and Hi 8 mm tapes. For protection against the elements, the camera was placed inside a toolbox that had a plexiglass window and mounted on a tripod. The camera was set up approximately 1 m from low nests and, if possible, positioned so that the nestlings were visible. To allow the catbirds to habituate to the video camera, a toolbox mounted on a tripod was set up at 12 nests for one to four days before each nest was actually videotaped. It soon became apparent that the adults returned to the nests even without the dummy set-up (see Appendix 5 for statistical test); thus this procedure was discontinued.

Videotape analysis

The initial period that the birds may have been agitated from the disturbance of the video camera was omitted from the observation time (see Clark and Lee 1998); observation time was calculated from the first feeding or brooding visit until the tape ended. If the nest was not clearly visible, it was not always possible to distinguish feeding visits from other visits. If possible, the amount of food brought per feeding trip (i.e., food load) was assessed using Price's (1998) method: 1 = did not show outside bill, 2 = projected over less than one-quarter of a bill, 3 = projected over one-quarter to a half of a bill, 4 = projected over one-half to three-quarters of a bill, and 5 = projected along the entire bill. Catbirds usually could not be sexed. Because only females typically brood the young (Johnson and Best 1982), all birds that brooded the nestlings were assumed to be female. That the same individual always brooded or shaded the nestlings was confirmed by observations of 6 pairs in which one member was aluminum or colour-banded.

Data analysis

Paired t-tests were used to test whether the following variables differed significantly between males and females: visitation rate, feeding rate, food load, and percentage of time spent at nest. T-tests were used to test whether the presence of a cowbird chick affected: visitation rate (female, male, and combined), feeding rate (female, male, and combined), female food load, and the percentage of time spent at the nest. The assumption of normality was valid in all cases (Shapiro-Wilk tests), and the assumption of equal variances was valid in all cases (Levene's test for equality of variances). The arc sine square root transformation for proportional data (Neter et al. 1990:621) was used on percentage of time spent at nest. Mann-Whitney tests were used to test whether the presence of a cowbird chick affected mean food load and male food load because the distributions of these variables were not normal. Male and female visitation and feeding rates were calculated only if the sex of the adult bird was known for all visits and feedings at a given nest. The mean male and female food loads were calculated based on those visits when the sex of the feeder was known, and did not necessitate knowing the sex of the adult feeder for all feeding visits. The overall mean food loads included food loads delivered by males, females, and adults whose sex was unknown. An alpha of 0.05 was used in all statistical tests.

RESULTS

Forty-five of 57 videotapes of nests could be analyzed for parental feeding visits, 33 of which were control nests and 12 of which contained a cowbird chick. The remaining 12 videos could not be analyzed because: 1) the catbirds did not return to the nest, 2) the catbird(s) alarm called for the entire duration of the video, or 3) the catbird(s) was visibly disturbed during the taping. For example, one catbird repeatedly flew at the camera, and another repeatedly performed the Head-up Fluffed Display posture, which

is an agonistic display (Harcus 1973). The use of a dummy video camera did not affect the probability of the catbirds being disturbed by the video camera (Appendix 5).

Catbirds took a mean of 7.7 (± 1.0) minutes after the video camera had been set up to feed or brood the young ($n = 45$).

Although the visitation rates did not differ between the sexes, males fed at a significantly higher rate than females and delivered more food to the nestlings with each visit (Table 8, Figure 9). Females spent a greater percentage of time at the nest than males (Figure 9). Most of the time, catbirds brought more than one food item at a time, so it was difficult to determine the type of food being fed to the chicks. Chironomids likely made up most of the multiple food item loads because they are the most abundant prey group at Delta Marsh (Busby and Sealy 1979, Briskie and Sealy 1989) and because they are slow-moving, several can be captured during one feeding trip (Biermann and Sealy 1982). Some single insect loads that were identified included: mayflies (Ephemeroptera), dragonflies (Odonata), geometrid larvae (Lepidoptera), moths (Lepidoptera), and mosquitoes (Diptera, Culicidae).

The presence of a cowbird chick increased both visit (Figure 10) and feeding rates (Figure 11), but the difference was significant only in terms of overall and female feeding rates (Table 9). The lack of significant effect of the cowbird chick on the visitation rate may be due to low power (less than 35% for all three tests). The increase in the overall feeding rate is probably entirely due to the increased female feeding rate because the male feeding rate was not affected by the presence of a cowbird chick (Figure 11). The amount of food brought with each feeding visit (Figure 12) and the amount of time spent at the nest by males and females (Figure 13) were not significantly affected by whether a cowbird chick was present.

Table 8. Statistical comparison of visit and feeding rates for male and female Gray Catbirds.

	t	df	P-value
Visitation rate	0.44	9	0.67
Feeding rate	2.69	9	0.02
Food load	2.44	23	0.02
% time spent at nest	6.88	9	< 0.0005

Figure 9. A, the visitation rate for female and male Gray Catbirds ($n = 10$). B, the feeding rate for female and male catbirds ($n = 10$). C, the food load for female and male catbird ($n = 24$). D, percentage of time spent at nest by female and male catbirds ($n = 10$). Food load was assessed using Price's (1998) method: 1 = did not show outside bill, 2 = projected over less than one-quarter of a bill, 3 = projected over one-quarter to a half of a bill, 4 = projected over one-half to three-quarters of a bill, and 5 = projected along the entire bill. Error bars = standard error.

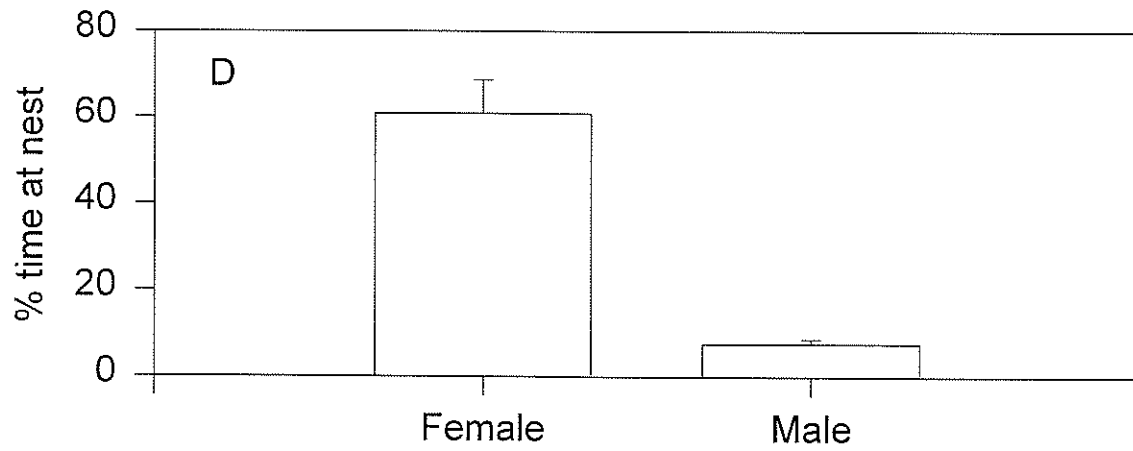
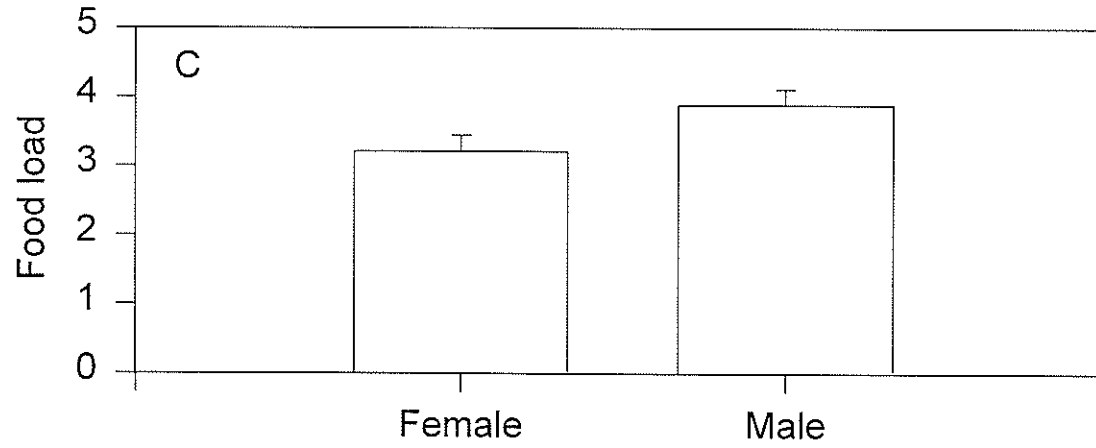
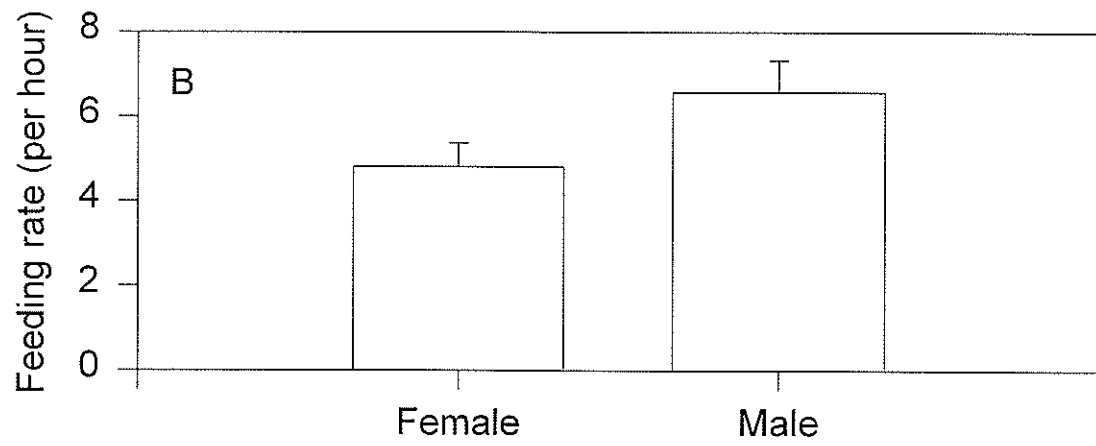
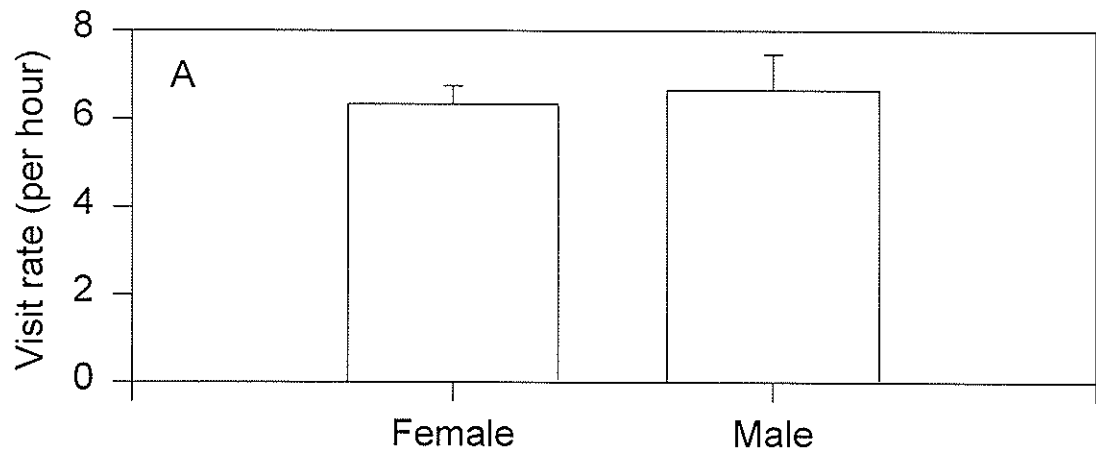
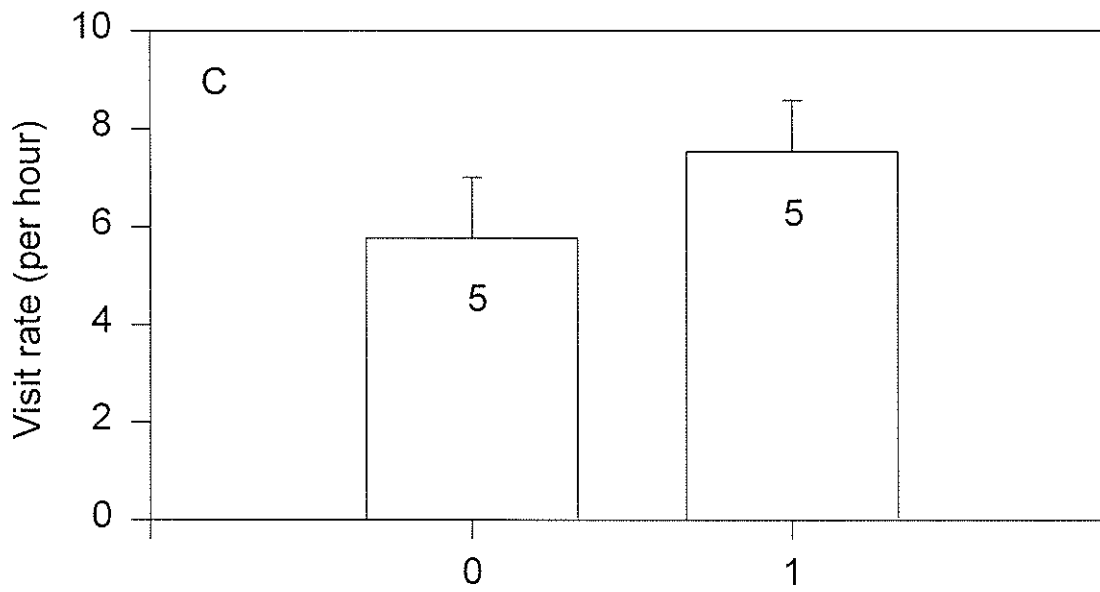
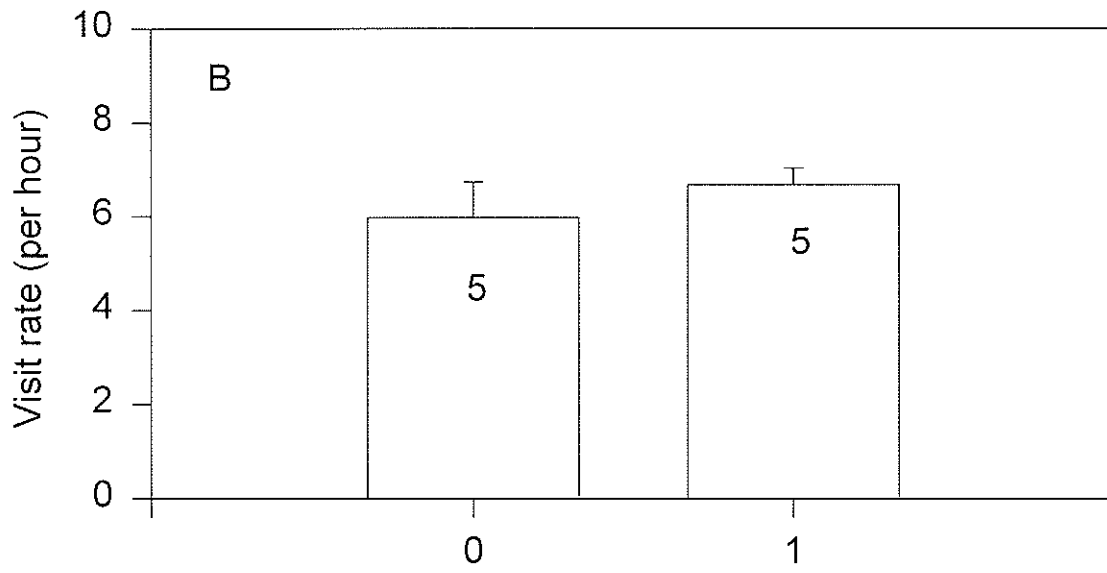
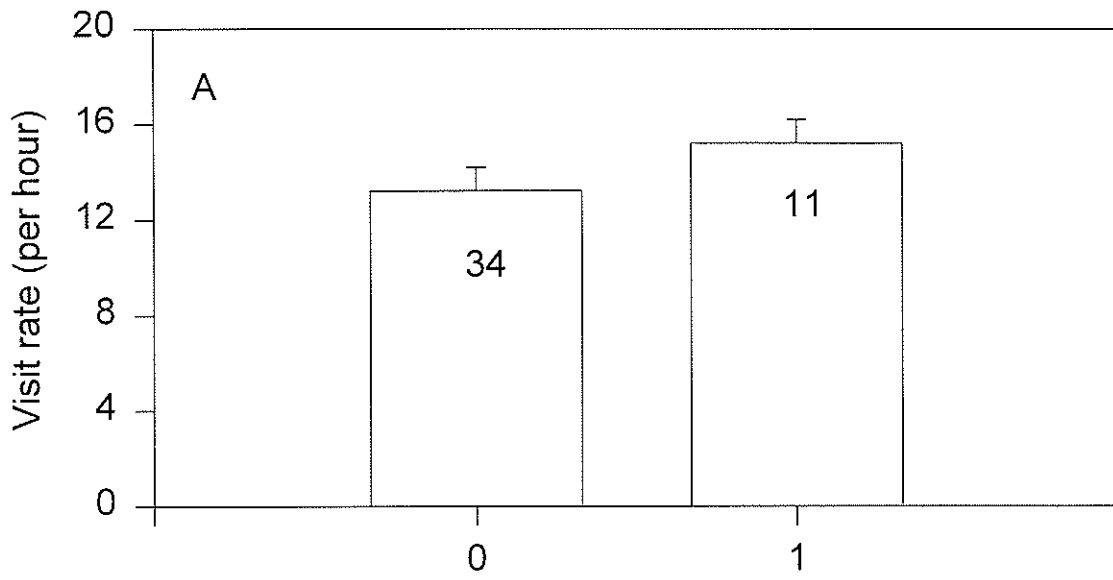


Figure 10. A, the effect of the presence of a Brown-headed Cowbird on overall nest visitation rate by adult Gray Catbirds. B, the effect of a cowbird chick on female visitation rate. C, the effect of a cowbird chick on male visitation rate. Sample sizes are provided on the graph. Error bars = standard error.



Number of cowbird chicks

Figure 11. A, the effect of the presence of a Brown-headed Cowbird on overall feeding rate by Gray Catbird adults. B, the effect of a cowbird chick on female feeding rate. C, the effect of the presence of a cowbird chick on male feeding rate. Sample sizes are provided on the graph. Error bars = standard error.

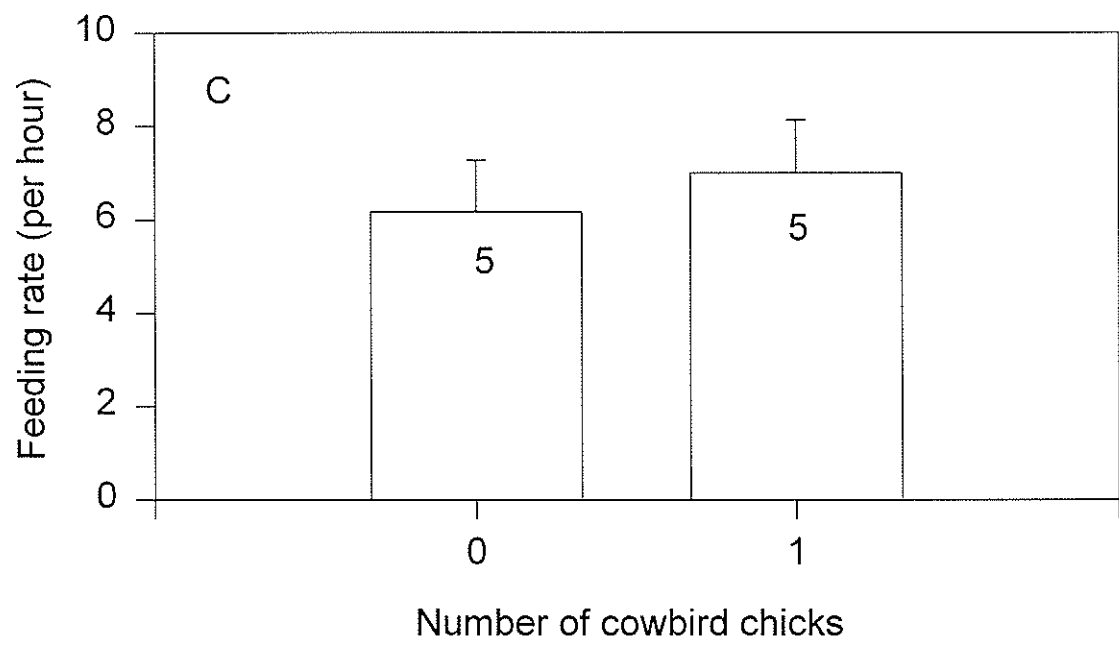
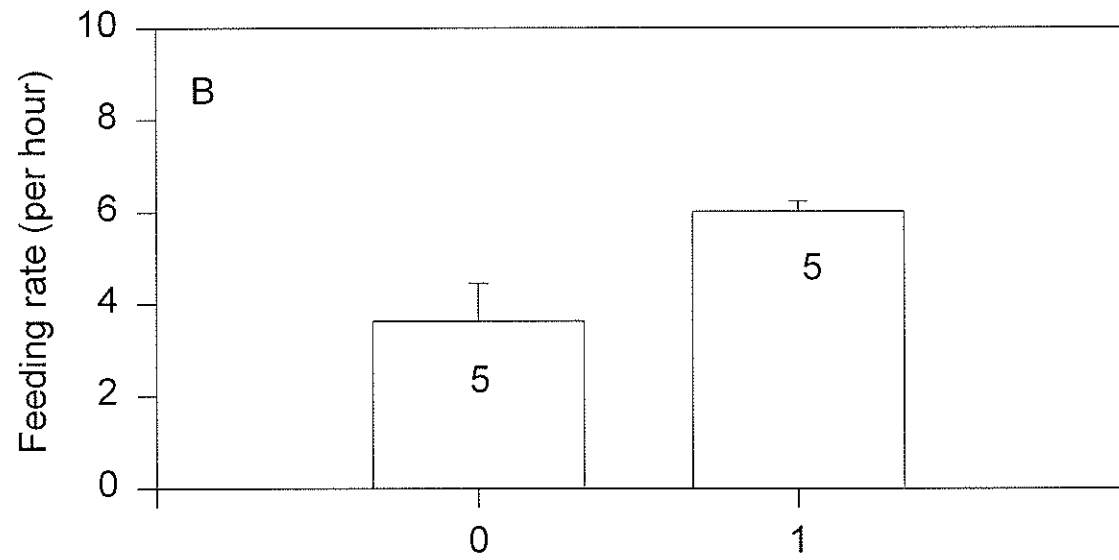
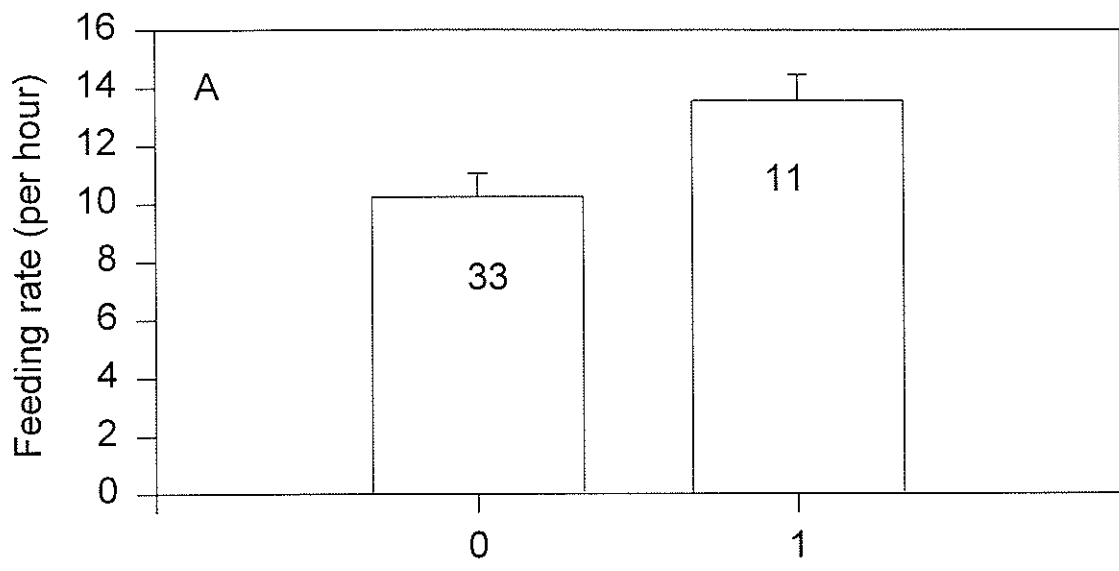


Table 9. Statistical comparison of various parental feeding parameters for Gray Catbird nests that were and were not parasitized experimentally by Brown-headed Cowbirds.

	t	df	P-value
Overall visitation rate	1.08	43	0.28
Male visit rate	1.08	8	0.31
Female visitation rate	-0.85	8	0.42
Overall feeding rate	2.20	42	0.03
Male feeding rate	-0.52	8	0.61
Female feeding rate	2.78	8	0.02
Overall food load ¹	n/a	n/a	0.40
Female food load	1.10	33	0.28
Male food load ¹	n/a	n/a	0.65
% time at nest by female	0.32	8	0.76
% time at nest by male	-0.78	8	0.46

¹ Mann-Whitney U test.

Figure 12. A, the effect of the presence of a Brown-headed Cowbird on overall food load in Gray Catbird nests. B, the effect of a cowbird chick on female food load. C, the effect of a cowbird chick on male food load. Food load was assessed using Price's (1998) method: 1 = did not show outside bill, 2 = projected over less than one-quarter of a bill, 3 = projected over one-quarter to a half of a bill, 4 = projected over one-half to three-quarters of a bill, and 5 = projected along the entire bill. Sample sizes are provided on the graph. Sample sizes are not equivalent for the same treatment because at some nests, the food load was only quantifiable for either the female or the male. Females were often easier to identify than males if they brooded directly after feeding. Error bars = standard error.

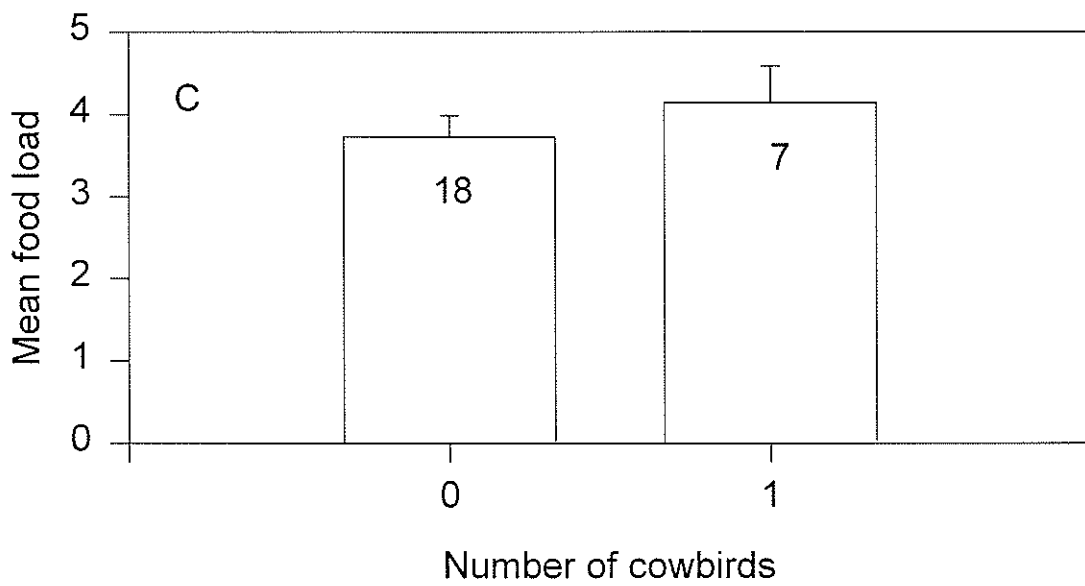
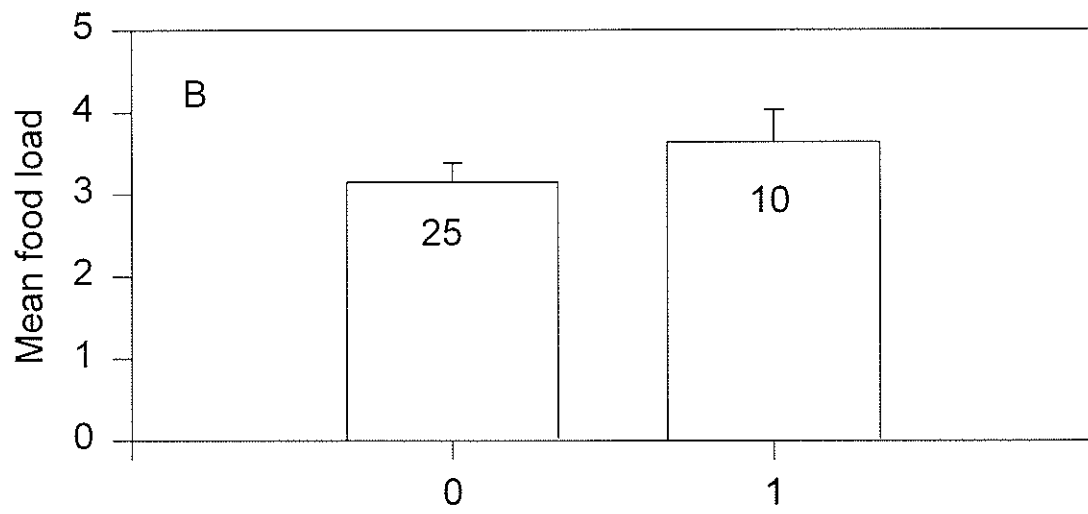
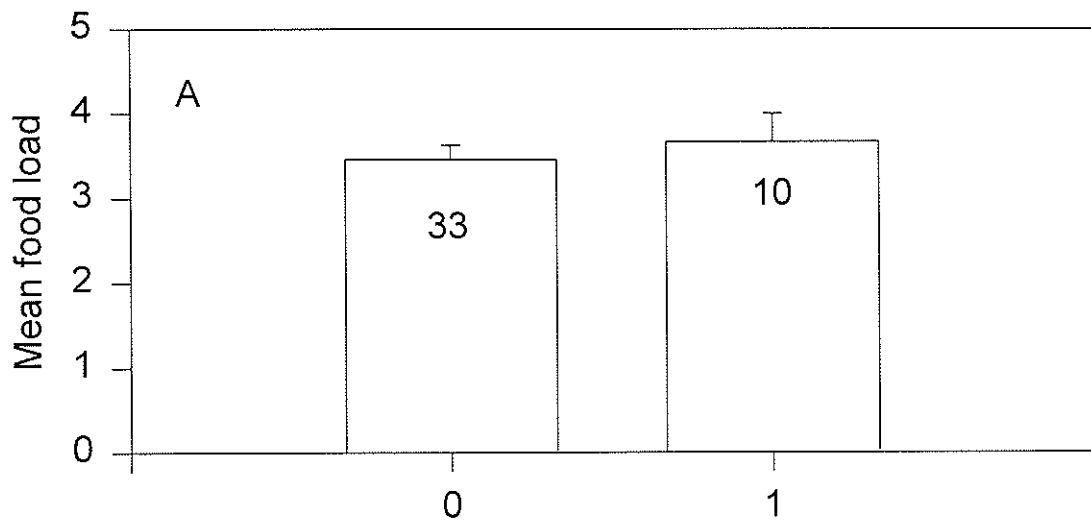
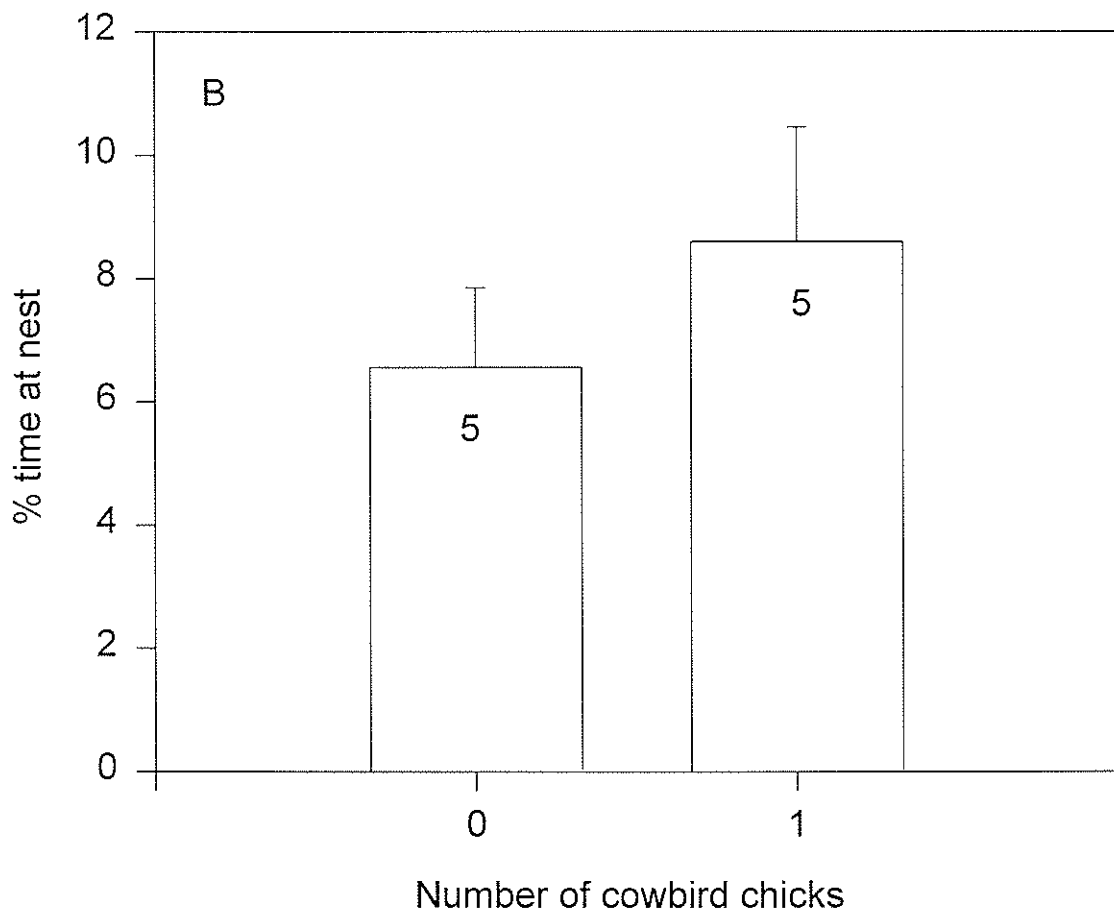
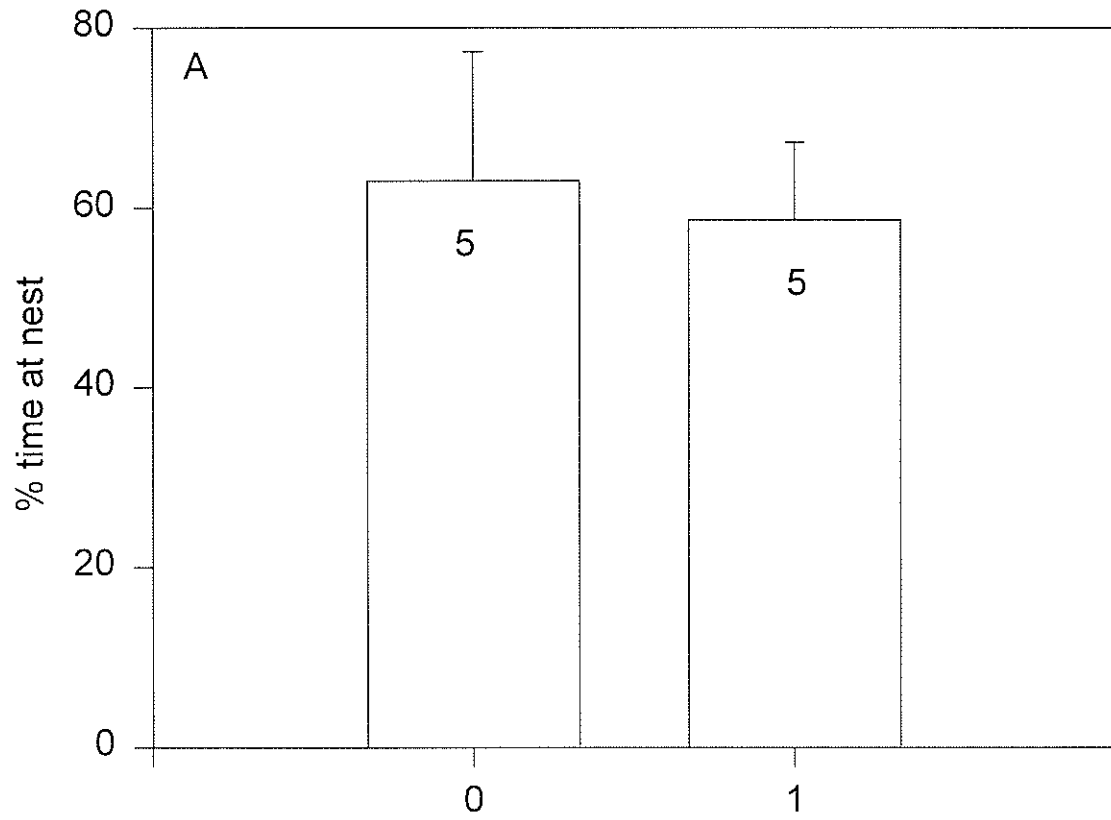


Figure 13. A, the effect of a Brown-headed Cowbird chick on the percentage of time spent at nest by female Gray Catbirds. B, the effect of a cowbird chick on the percentage of time spent at nest by male catbirds. Sample sizes are provided on the graph. Error bars = standard error.



DISCUSSION

Both the overall visitation rates (Figure 10) and feeding rates (Figure 11) increased when a cowbird chick was present in a catbird nest, but only the difference in feeding rates was significant. Feeding rates were also greater at parasitized Indigo Bunting (*Passerina cyanea*) nests (Dearborn et al. 1998), but not at parasitized Red-winged Blackbird nests (Clotfelter 1997). The increase in overall feeding rate at catbird nests was due to the increase in female feeding rate and not an increase in male feeding rate. The increase in feeding rate by females did not result in a trade-off in the amount of food brought to the nest with each visit (Figure 12b). Interestingly, the opposite trend was found for both females and males, with a greater volume of food per feeding visit being brought to nests that contained a cowbird chick. Therefore, the amount of work done by female catbirds to provision nests increased in two ways. However, the quality of food was not assessed; therefore, it is possible that females brought more lower-quality food to parasitized nests. When the brood's demand for food was increased in other studies, parents fed a larger proportion of small prey, which were easier to capture and were interpreted as being low in quality (Royama 1966, Tinbergen 1981, Lifjeld 1988).

Even though female provisioning rate increased in response to the presence of the cowbird chick, the amount of time female catbirds spent at the nest was not affected (Figure 13). Dearborn et al. (1998) found similar results with female Indigo Buntings. Perhaps because females spent more time at the nest than males (Figure 9d), they were better able to identify a need for increased provisioning when a cowbird chick is present. An increase in begging call rate could be an example of a cue. Henderson (1975) was the first to suggest that the calling rate of the brood affected parental feeding rate. More recently, begging calls have been experimentally demonstrated to effect parental feeding

rate (Bengtsson and Rydén 1983, Burford et al. 1998, Price 1998, but see Clark and Lee 1998). Indeed, although begging calls were not quantified in this study, nestlings seemed to call louder and more often in parasitized nests.

The increased level of vocalization in parasitized nests may be due to a high call rate by the cowbird chick alone, the catbird chicks alone, or both. Lorenzana (1996) suggested that the cowbird's polysyllabic begging call may mimic the begging call of hungry chicks by compressing more monosyllabic begging calls into a given length of time. Similarly, Davies et al. (1998) suggested that nestling Common Cuckoos (*Cuculus canorus*) mimic the begging calls of an entire brood, which may be necessary to obtain adequate care because it ejects host eggs and young from the nest and is reared alone.

Individuals increase their level of begging in response to increased begging levels of nestmates (e.g., Smith and Montgomerie 1991, Price and Ydenberg 1995) or experimental playbacks of begging calls (e.g., Muller and Smith 1978); therefore, catbird chicks may have increased their begging rate in response to the high level of vocalization by the cowbird chick. Food deprivation results in an increase in begging intensity (e.g., Bengtsson and Rydén 1983, Smith and Montgomerie 1991, Price and Ydenberg 1995, Hofstetter and Ritchison 1998). However, catbird chicks in parasitized nests were not food deprived (Chapter 3), therefore, there is no reason to believe that increased vocalizations were due to food deprivation.

By increasing the volume of food brought to parasitized nests, female catbirds minimized the costs of parasitism that were incurred by catbird chicks. In fact, catbird chicks in parasitized and unparasitized nests on day 4 post-hatch did not receive significantly different amounts of food (Chapter 3). Presumably, the female catbirds incurred a cost as a result of their increased provisioning rates. It is assumed that current reproductive effort reduces future reproductive effort through increased adult mortality during or after the breeding season or through a decrease in future

reproductive investment (Stearns 1992). Increased adult mortality may result from an increased risk of predation from foraging in a less vigilant manner (Dearborn et al. 1998) or from being more vulnerable to predation or illness due to being in poor condition. Payne and Payne (1998) did not find that survival or reproductive success of Indigo Buntings was affected by parasitism in the previous year, and concluded that nearly all costs of parasitism are manifested in the parasitized brood. A limitation of their study is that they assessed long-term costs by considering the survivorship and fecundity of females in the next year; they did not consider the lifetime cumulative effects of parasitism. The cost of caring for larger broods has been examined in other studies. Nur (1988:165) reviewed both experimental and non-experimental evidence on this topic and concluded that "the evidence is rather good" that birds rearing larger broods suffer from decreased survival and/or decreased future fecundity. For example, Askenmo (1979) found that Pied Flycatcher (*Ficedula hypoleuca*) males caring for experimentally enlarged broods had reduced survival rate, presumably due to the increased work involved with feeding a larger brood.

In summary, female catbirds increased their feeding rate in response to the presence of a cowbird chick, but males did not. The increase in feeding rate by the female was not accompanied by a significant increase in visitation rate, nor did it affect the amount of time spent brooding. Interestingly, both male and female catbirds brought slightly more food during each trip to parasitized nests, although the quality of the food was not assessed. Because female catbirds need to work harder to provision parasitized nests, it is possible that female catbirds experience a future cost of parasitism; however, no conclusive evidence that this is the case is provided in this study, nor does it mean that males do not incur a future cost of parasitism. A better test of this hypothesis would be to conduct a study similar to Payne and Payne (1997). By

working with a banded population of catbirds, one could determine whether parasitism affects the return rates and the fecundity of individuals that breed the following year.

Chapter 3. Competitive interactions between catbird and cowbird chicks

In studies of small hosts, cowbird chicks were fed up to twice as much as their host nestmates (Dearborn 1998, Lichtenstein and Sealy 1998). Cowbirds may present exaggerated features, such as a different coloured gape, that are preferred by the host adults (supernormal stimulus hypothesis) (Dawkins and Krebs 1979). Researchers interpret the components of the supernormal stimulus hypothesis in different ways. Tinbergen (1951) considered as supernormal any stimuli that are more effective than normal ones. Soler et al. (1995) identified Great Spotted Cuckoos (*Clamator glandarius*) with supernormal stimuli because they are preferentially fed over Black-billed Magpie (*Pica pica*) nestmates. They considered large size, intense begging, and conspicuous palatal papillae to be supernormal stimuli. Lichtenstein and Sealy (1998), however, did not consider as supernormal stimuli any components of begging behaviour such as posturing and relative height reached that would give the parasitic chick a physical advantage over the host's young. If parasitic young were preferred because they outcompeted host nestlings using a physical advantage, Lichtenstein and Sealy (1998) interpreted this as support for the competition hypothesis rather than the supernormal stimulus hypothesis. Conspicuous palatal papillae, which are not found in magpie nestlings, would be considered a supernormal stimulus under Lichtenstein and Sealy's (1998) definition if the cuckoos that displayed them were fed preferentially.

In this chapter, I will interpret my results in the manner used by Lichtenstein and Sealy (1998) because I can differentiate between whether parasitic nestlings are preferred because they exaggerate the signals that adults usually use in allocating food to nestlings or whether they use a different stimulus altogether. Adults prefer to feed nestlings that beg in a certain way, such as those that reach the highest or beg first (e.g., Smith and Montgomerie 1991, Teather 1992, Price and Ydenberg 1995, Leonard and

Horn 1996). If the competition hypothesis applies, the cowbird chick should be fed when it displays the characteristic(s) that adults prefer, in the present case, Gray Catbirds. The supernormal stimulus hypothesis predicts that the cowbird nestling would be fed regardless of whether it displays the characteristics that the adult catbirds prefer.

Dearborn (1998) identified three other hypotheses to explain why cowbirds are preferentially fed. The size advantage hypothesis: cowbirds are preferentially fed due to the direct or indirect effects of their larger body size. The signal exaggeration hypothesis: cowbirds are fed more because they produce exaggerated signals, independent of body size, that are normally used by host parents in assessing the needs of host nestlings (e.g., begging longer or during a greater proportion of feeding visits). The novel begging behaviour hypothesis: cowbirds are fed more because they exhibit novel begging behaviours. The size advantage and signal exaggeration hypotheses are essentially the same as the competition hypothesis, except that there is a distinction between whether the cues used in eliciting feedings are dependent on body size. The novel begging behaviour hypothesis is essentially the supernormal stimulus hypothesis.

The competitive interactions of cowbird chicks and their host nestmates have been assessed in only two published studies (Dearborn 1998, Lichtenstein and Sealy 1998). There was support for the competition hypothesis in both studies. Because these studies involved hosts that were half the size of the cowbird chick, in the present study, I should be able to determine whether competitive interactions differ when the cowbird chick is only slightly larger than the host chick.

My goal was to examine the intricacies of the competition that affected the amount of food obtained by catbird and cowbird nestlings. Assessing the competitive ability of the cowbird chick relative to the catbird chick, however, is only one part of the story. The first objective was to determine whether cowbird chicks are fed more than catbird chicks. Having determined this, my next objective was to determine whether

cowbird chicks begged more often than catbird chicks and/or whether cowbird chicks had a greater probability of being fed than catbird chicks. If cowbird chicks were more likely to be fed than catbird chicks, the third objective was to determine whether cowbird chicks are better competitors than catbird chicks or whether they present supernormal stimuli. The fourth objective was to examine the effect of the presence of the cowbird chick on the amount of food obtained by catbird chicks. Because the effect of parasitism may differ depending on the hatching order of the catbird chicks, catbird chicks that hatched on the first day were designated as core chicks, and all other chicks were designated as marginal chicks (see Forbes et al. 1997). The fifth objective was to determine the proximal reasons for the amount of food that catbird chicks received in parasitized nests relative to those in unparasitized nests. For example, do catbird chicks in parasitized nests beg more often than catbird chicks in unparasitized nests? Does the increase in feeding rate exhibited by females (Chapter 2) compensate for the extra competition that the cowbird chick provides?

METHODS

This project was conducted from mid-May to early July 1998 at Delta Marsh, Manitoba. See General Introduction for more details about the study site. Newly hatched cowbird chicks were placed into catbird nests generally one to two days before the catbird chicks hatched. See Chapter 1 for more details about how cowbird chicks were obtained. See Chapter 2 for information regarding how nests were video-taped. Not all nests that were analyzed in Chapter 2 for visitation rates were analyzed in terms of which nestlings were fed because there was not always a clear view into the nest. Nestling heads of both species were painted randomly with different colours of non-toxic acrylic paint so that the identity of individual nestlings could be determined while watching the video. Paint colour did not affect the competitive ability of the chicks

(Appendix 6). Chicks were massed and measured on the same day they were videotaped.

Catbird and cowbird chicks in each brood were ranked in terms of the sequence of begging initiation (start rank), relative height (height rank), and relative distance between parent's and nestling's beak tips (beak rank). For example, the nestling that started begging first received a start rank of 1. Nestlings that tied received the average of the ranks for which they were tied. For example, if two nestlings tied at being first to initiate begging, they would both receive a start rank of 1.5. Nestlings that did not beg were not ranked. Ranks were assigned at the moment just prior to when the adult offered food to a nestling (see Teather 1992). Ranks were standardized using $[(\text{rank} - 1)/(\text{number that begged} - 1)]$ to make ranks comparable between nests of different brood sizes (Teather 1992). Begging intensity was categorized into one of 4 levels: 1) bill opened, tarsi flexed, 2) neck stretched, tarsi flexed, 3) neck stretched, tarsi extended, and 4) wing (see Lichtenstein and Sealy 1998). An *offering* was made when a parent placed food into the mouth of a chick (if only temporarily) and *feeding* occurred when a chick actually ingested the food. By definition, a chick that was fed also received an offering.

Data analysis

SPSS version 8.0 was used to perform all statistical analyses. An alpha of 0.05 was used in all statistical tests. The success of competitive interactions between nestlings was assessed in terms of first food offers. The nestling that received the first food offering had the first chance at ingesting the food, and presumably would lose the feeding opportunity only if it was already satiated (Teather 1992), or if the food item was too big (Reed 1981, pers. obs.). In those cases when food was delivered to two or more

chicks during one feeding bout, the chick that was first offered food generally ingested more food than any nestlings fed subsequently (pers. obs.).

Separate ANOVA tests were used to test whether the following variables are different for cowbird chicks, core chicks in parasitized and unparasitized nests, and marginal chicks in parasitized and unparasitized nests: 1) the number of feedings obtained per hour, 2) size of food received during each food transfer (i.e., food load), 3) the proportion of feeding visits in which begging occurred by a given nestling, and 4) the probability of obtaining a first food offer. Only nestlings that begged during more than one feeding visit that had competition were included in the calculation of the probability of obtaining a first food offer. The arc sine square root transformation for proportional data (Neter et al. 1990:621) was used on the proportion of feeding visits begged and on the probability of obtaining a first food offer. If the difference was significant, the Tukey method was used to determine which pairwise comparisons were significant. The Tukey method was used because this method adjusts the observed significance level because multiple comparisons are made, and it gives narrower confidence intervals than the Scheffé and Bonferroni methods when a large number pairwise comparisons are of interest (Neter et al. 1990:587, 589). I was particularly interested in comparisons between different nestling types in the same nest and the same nestling types in different nests. The experimental unit was the nest; therefore, the means of the above variables were calculated for core and marginal nestlings for each nest.

Separate ANOVAs were used to test whether the following begging indices were different for cowbird chicks, core chicks in parasitized and unparasitized nests, and marginal chicks in parasitized and unparasitized nests: start rank, height rank, beak rank, begging intensity, and tarsus length. If the difference was significant, the Tukey method was used to determine which pair-wise comparisons were significant. The arc sine square root transformation for proportional data (Neter et al. 1990:621) was used on

start rank, height rank, and beak rank because the ranks were standardized such that they would vary from 0 to 1. Mass was not analyzed because it is highly correlated with tarsus length (Pearson correlation = 0.913).

A stepwise multivariate regression analysis was used to determine which of the following variables were important in determining which catbird chick received the first food offering in an unparasitized brood: tarsus length, mass, start rank, height rank, beak rank, and begging intensity. A second stepwise regression analysis was used to determine whether the same variables, in addition to whether the chick was a catbird or a cowbird, were important in determining which chick in a *parasitized* brood received the first food offering. In both stepwise regression analyses, variables were entered if probability-of-F ≤ 0.05 , and variables were removed if probability-of-F ≥ 0.10 . The experimental unit was the nest; therefore, means for the above variables for each nestling type were calculated for each nest.

RESULTS

Thirty-one videos could be analyzed in terms of which nestling was fed. A mean of 60.3% ($\pm 5.2\%$) of the feeding visits involved more than one nestling begging. In a mean of 35.3% ($\pm 4.8\%$) of the feeding visits, more than one nestling was offered food, and in a mean of 28.3% ($\pm 4.6\%$) of the feeding visits, more than one nestling ingested some food. Nestlings ingested a mean of 90.2% ($\pm 2.3\%$) of all offered food.

Are cowbird chicks fed more than catbird chicks?

Cowbird nestlings obtained more than twice as many feedings as core and marginal catbird chicks in parasitized nests (Figure 14a), and this difference was statistically significant (Table 10, Appendix 8). There was no significant difference among any of the nestlings in terms the amount of food obtained during each feeding

Figure 14. The effect of nestling type (i.e., cowbird, core unparasitized catbird, marginal unparasitized catbird, core parasitized catbird, and marginal parasitized catbird) on the A, number of feedings obtained per hour; B, food load; C, percentage of feeding visits begged, and D, probability of obtaining a first offer;). UC - core catbird chick in unparasitized nest (A - C: n = 23; D: n = 19)¹; UM - marginal catbird chick in unparasitized nest (A, C: n = 15; B: n = 13; D: n = 14)²; PC - core catbird chick in parasitized nest (n = 7); PM - marginal catbird chick in parasitized nest (n = 5); CB - cowbird chick (A - C, n = 7; D: n = 6). Error bars = standard error.

¹ The sample size for the probability of obtaining a first offer, D, is smaller than that in the other categories because it includes only nestlings that begged during more than one feeding visit with competition.

² The sample size for food load, B, is smaller than the other categories because a mean food load could not be calculated for two chicks that did not receive any feedings.

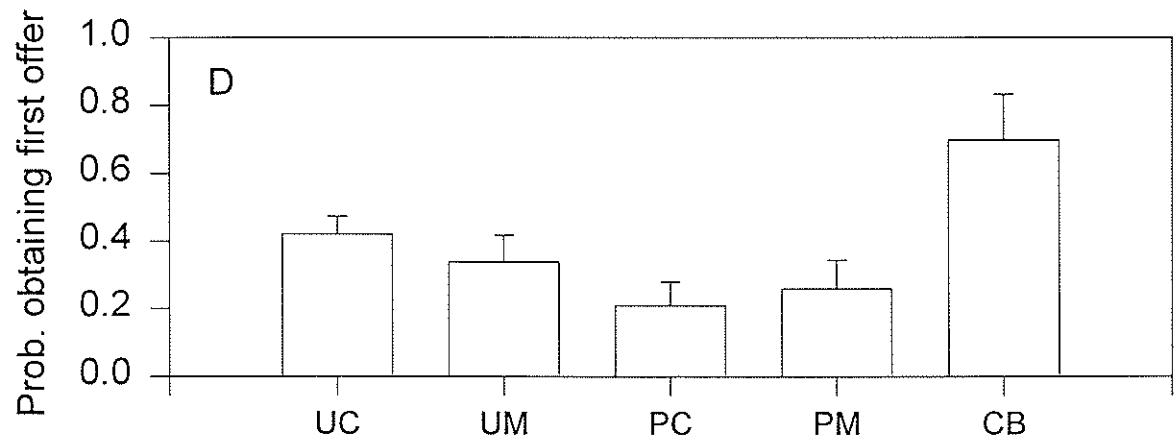
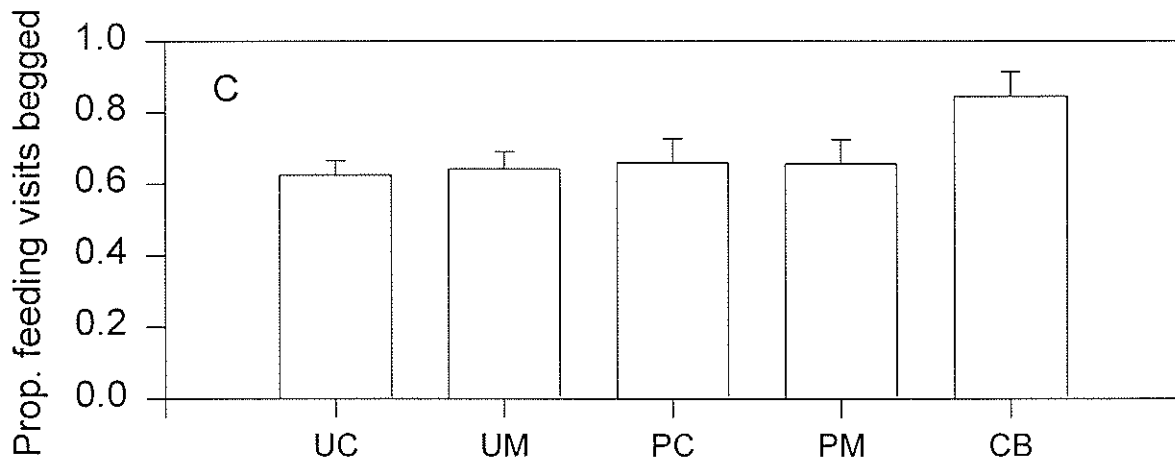
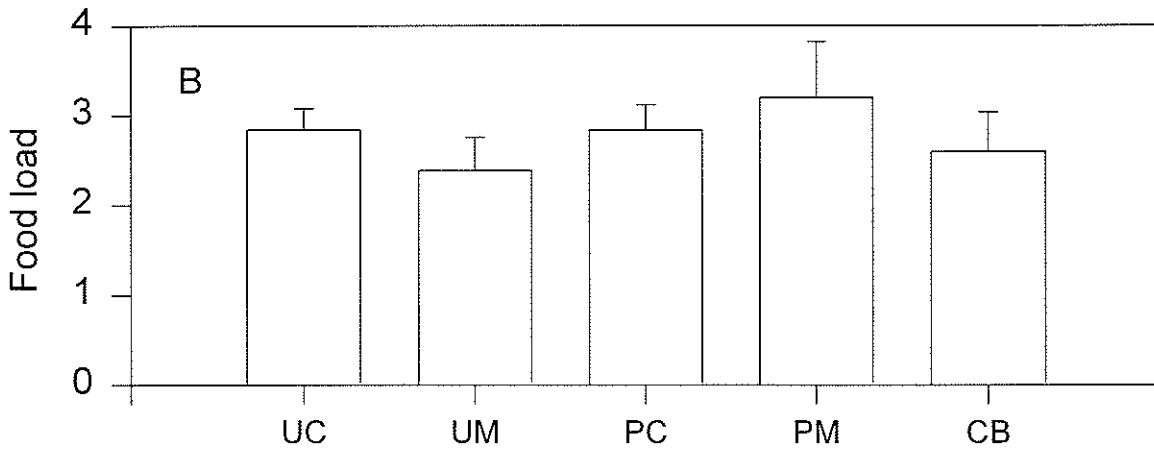
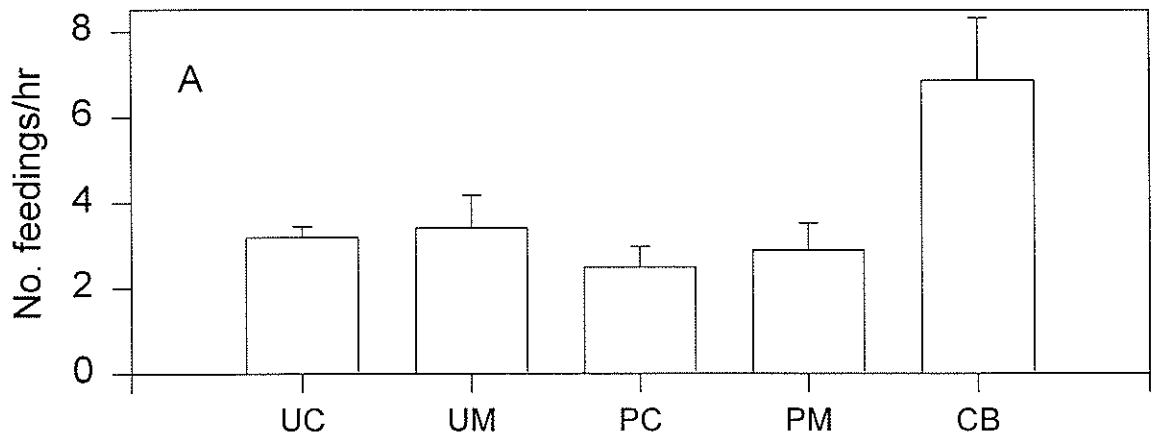


Table 10. Significance and power of the effect of nestling type (i.e., cowbird, core unparasitized catbird, marginal unparasitized catbird, core parasitized catbird, and marginal parasitized catbird) on the amount of food obtained.

Test	F-value	df	P-value	Power
Feedings/hr	4.661	4, 52	0.003	0.929
Food load	0.575	4, 50	0.682	0.178
Proportion of feeding visits begged ¹	2.018	4, 52	0.106	0.565
Probability of obtaining first food offer ¹	3.462	4, 46	0.015	0.820

¹ Arc sine square root transformed

visit (Table 10, Figure 14b); therefore, overall, cowbird chicks received twice as much food as catbird chicks.

Proximate mechanisms for why cowbird chicks were fed more than catbird chicks

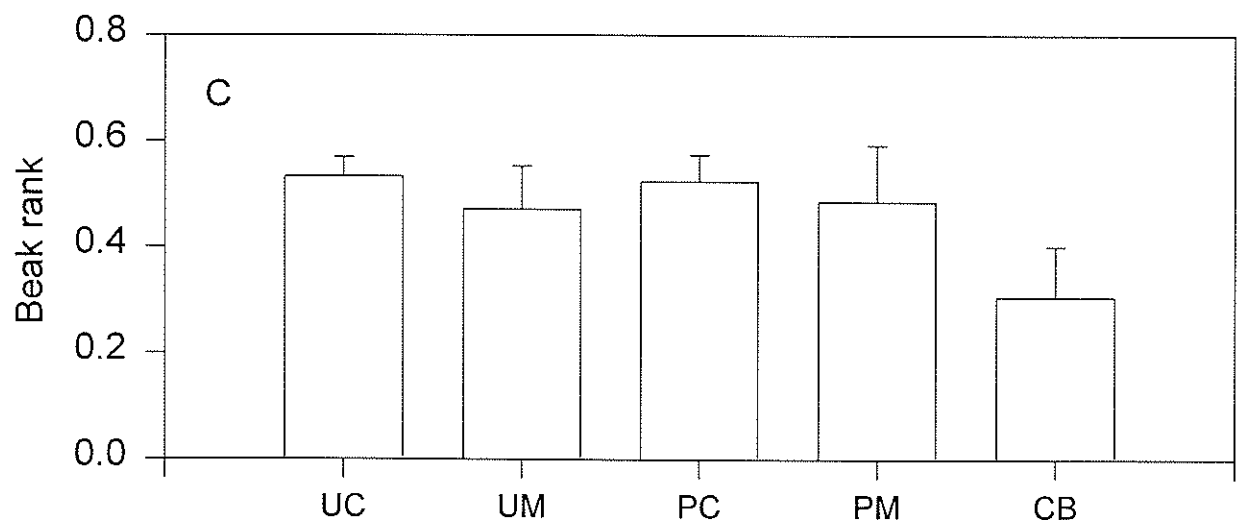
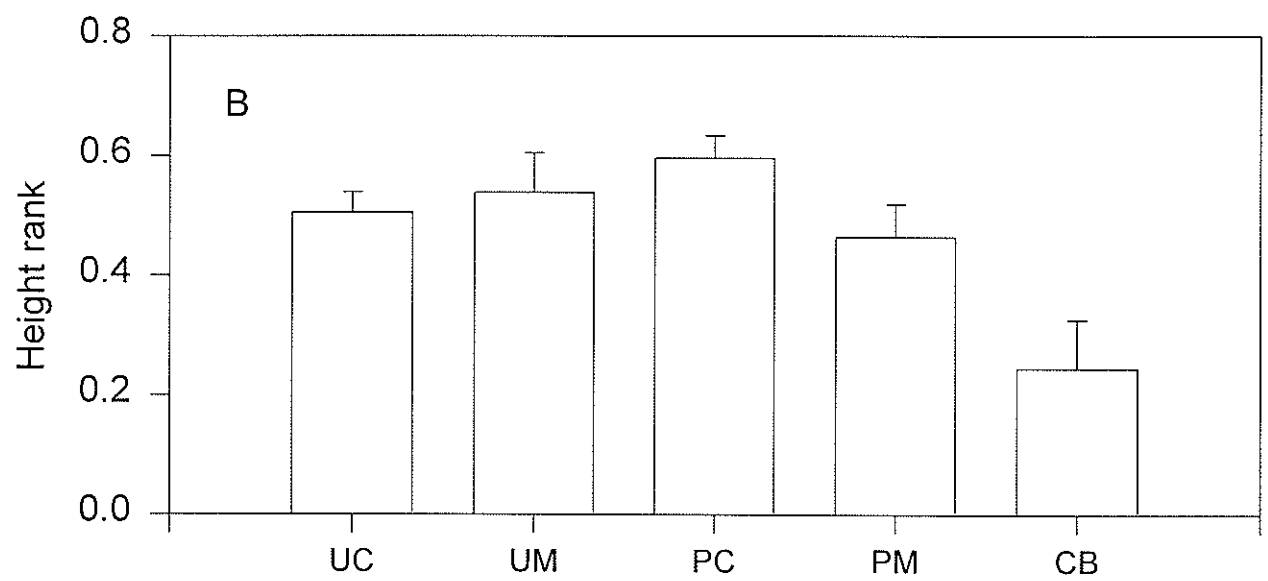
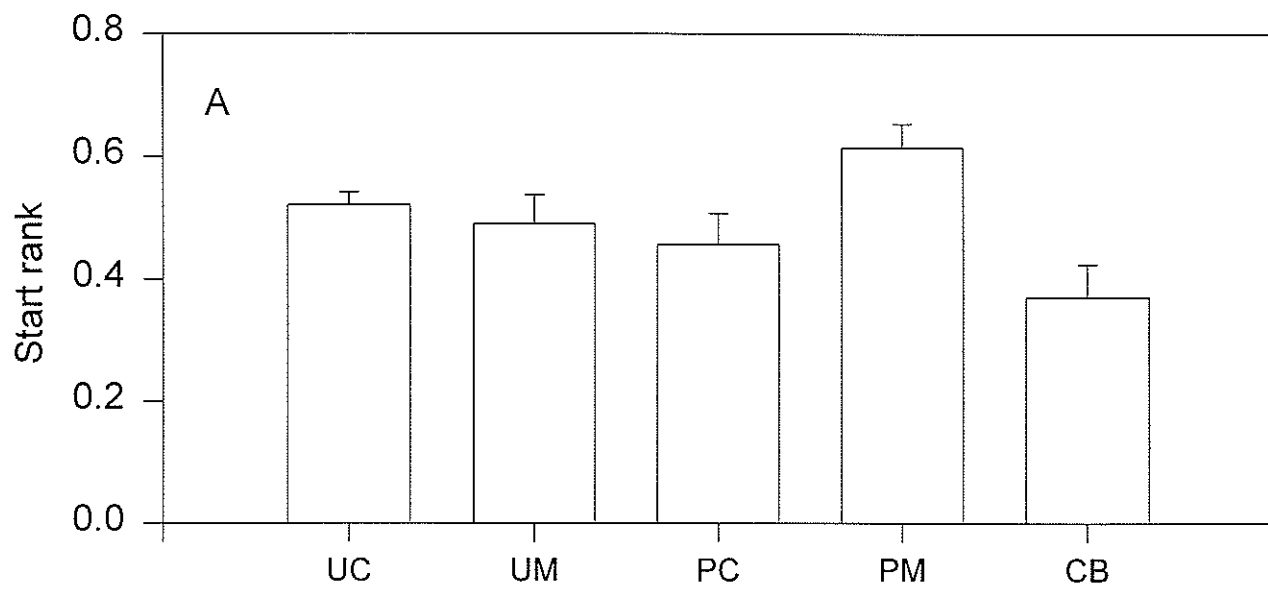
Cowbird chicks begged during a higher proportion of feeding visits than either the core or marginal chicks in parasitized nests (84.5% relative to 66.0% and 65.7%, respectively, Figure 14c). This difference, however, was not significant (Table 10). Cowbird chicks had 3 times the probability of being fed than catbird chicks in parasitized nests (Figure 14d), and this difference was statistically significant (Table 10, Appendix 9).

Why are cowbird chicks preferentially fed?

Cowbird nestlings generally begged before core and marginal catbird chicks in parasitized nests (Figure 15a), and this difference was significant between marginal and cowbird chicks (Table 11, Appendix 10). Cowbird nestlings reached higher than core and marginal catbird chicks (Figure 15b), and this difference was significant between core and cowbird chicks (Table 11, Appendix 11). Reaching higher than catbird nestlings probably aided cowbird nestlings in positioning their beaks closer to the beaks of feeding adults (Figure 15c), but the difference in beak-to-beak distance was not statistically significant (Table 11). Begging intensity did not differ significantly between cowbird and catbird nestlings in parasitized nests (Table 11). Both catbird and cowbirds had a mean begging intensity of approximately 2 (Figure 15d); i.e., nestlings normally begged by stretching their neck, without extending their tarsus. Therefore, cowbird nestlings reached higher than catbird nestlings simply due to their size advantage (Table 11, Figure 15e, f, Appendix 12).

Figure 15. The effect of nestling type (i.e., cowbird, core unparasitized catbird, marginal unparasitized catbird, core parasitized catbird, and marginal parasitized catbird) on the A, start rank; B, height rank; C, beak rank; D, begging intensity; E, tarsus length; F, mass. Ranks closer in value to 1.0 indicate nestlings with a slower start, a lower height, and a longer beak distance. UC - core catbird chick in unparasitized nest (A - D: n = 19; E - F: n = 23)¹; UM - marginal catbird chick in unparasitized nest (A - D: n = 14; E - F: n = 15); PC - core catbird chick in parasitized nest (A - D: n = 7; E - F: n = 9); PM - marginal catbird chick in parasitized nest (n = 5); CB - cowbird chick (A - D: n = 6; E - F: n = 8). Begging intensity: 1) gapes, tarsi flexed, 2) neck stretched, tarsi flexed, 3) neck stretched, tarsi extended, and 4) wing flapping. Error bars = standard error.

¹ Sample sizes differ because nestlings at all nests were massed and measured, but the begging ranks could not be established at all nests.



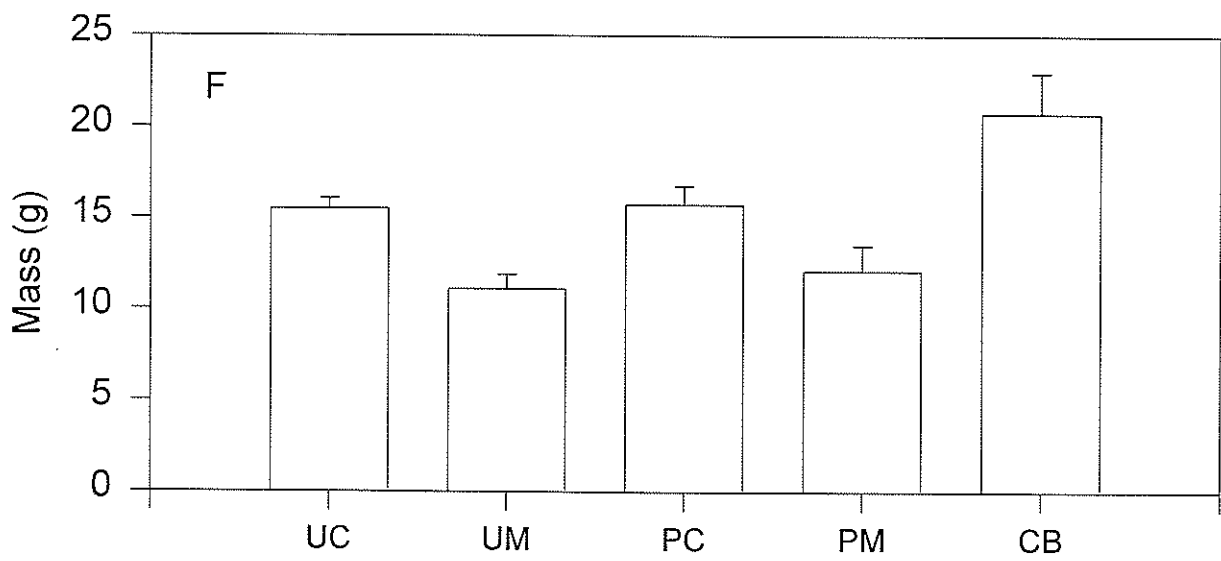
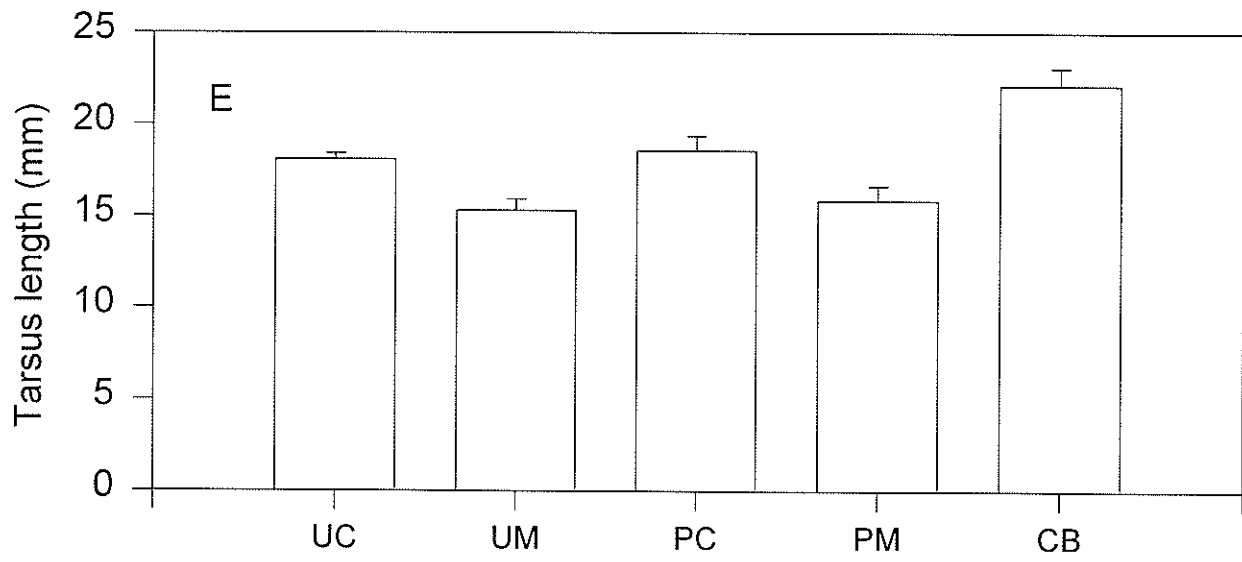
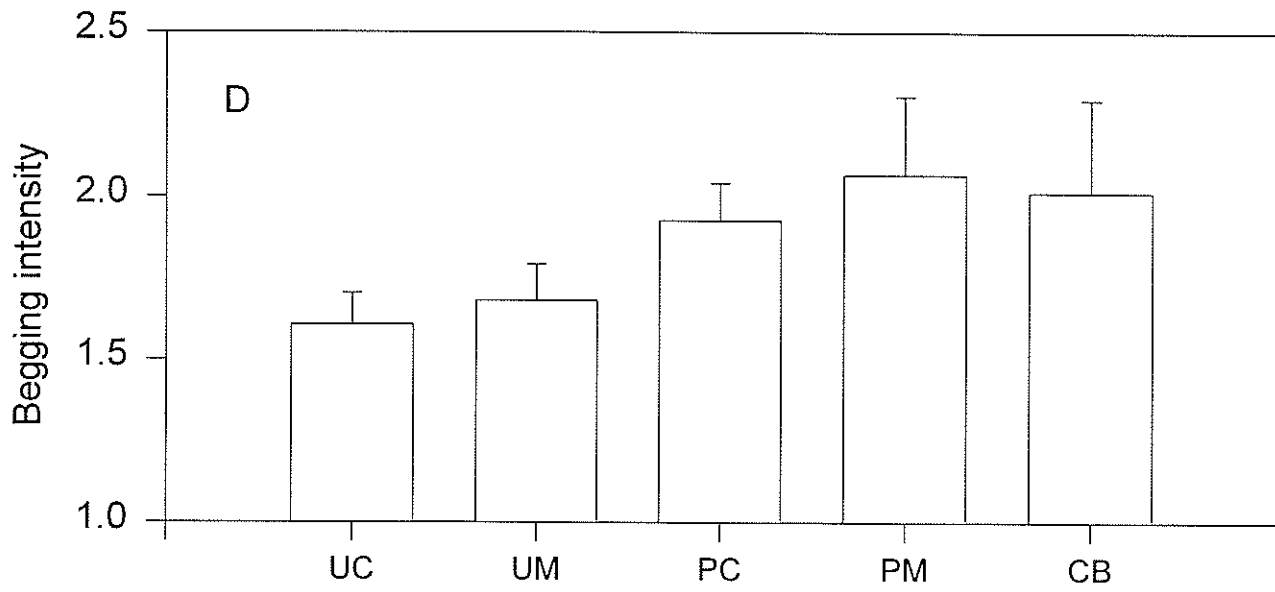


Table 11. Significance and power of the effect of nestling type (i.e., cowbird, core unparasitized catbird, marginal unparasitized catbird, core parasitized catbird, and marginal parasitized catbird) on begging ranks and size.

Test	F-value	df	P-value	Power
Start rank ¹	2.576	4, 46	0.050	0.680
Height rank ¹	3.658	4, 46	0.011	0.843
Beak rank ¹	1.350	4, 46	0.266	0.387
Begging intensity	1.888	4, 46	0.129	0.528
Tarsus length	15.147	4, 55	< 0.0005	1.000

¹ Arc sine square root transformed.

Height rank was the only variable that was important in predicting which chick was to be offered food in both unparasitized and parasitized nests. Height rank approached significance in unparasitized nests ($t = -1.911$, $P = 0.078$, Appendix 13) and was significant in parasitized nests ($F = 56.5$, $1, 11$, $P < 0.0005$, adjusted $R^2 = 0.82$). The significance of variables that were excluded from the models involving parasitized nests is shown in Appendix 14. The correlation between all of the variables in parasitized and unparasitized nests is shown in Appendix 15 and Appendix 16.

Does the presence of a cowbird chick affect food acquisition by catbird chicks?

Core and marginal catbird nestlings in parasitized and unparasitized nests did not differ significantly in terms of the number of feedings received per hour (Figure 14a, Appendix 8), or in terms of the amount of food received with each feeding (Figure 14b). Therefore, the presence of a cowbird chick did not affect food acquisition by catbird chicks on days 4 to 5 post-hatch.

Proximate mechanisms for why food acquisition by catbird chicks was not affected

The proportion of feeding visits begged by catbird chicks in parasitized and unparasitized nests did not differ significantly (Figure 14c, Table 10). Nonetheless, catbird chicks in parasitized nests begged more often than catbird chicks in unparasitized nests because there was a greater number of feeding visits at parasitized nests (Chapter 2, Figure 10). By multiplying the mean number of feeding visits by the proportion of feeding visits begged, catbird chicks in parasitized nests begged 8.9 times per hour and catbird chicks in unparasitized nests begged 6.38 (core) to 6.56 (marginal) times per hour. By begging more often, catbird chicks in parasitized nests received the same number of feedings per hour even though catbird nestlings in parasitized nests had a lower, but non-significant, probability of obtaining a first offer than catbird chicks in

unparasitized nests (Figure 14d, Appendix 9). Catbird chicks in parasitized nests begged at a higher intensity than catbirds in unparasitized nests (Figure 15d), with catbird chicks in parasitized nests stretching their neck more often when they begged than catbird chicks in unparasitized nests.

DISCUSSION

Competitive interactions between cowbird and catbird chicks

In this study, cowbird chicks obtained twice as much food as catbird chicks. Cowbird nestlings have been found to obtain twice as much food as host nestlings that are less than half their size (Dearborn 1998, Lichtenstein and Sealy 1998), but this is the first study that has demonstrated a cowbird chick outcompeting host nestmates that are not much smaller than themselves. Cowbird chicks begged sooner, reached higher, and were larger than catbird nestlings. Of the variables measured, height was the single most important parameter that determined which nestling, cowbird or catbird, was offered food first in both unparasitized and parasitized nests. Cowbird and catbird chicks generally begged with their necks stretched without extending their tarsi to increase their height. Therefore, cowbird chicks reached higher than catbird chicks simply because they were larger and not because they begged more intensely. These findings support the competition hypothesis. Cowbirds were fed preferentially because they generally reached higher than catbird chicks. Catbird adults preferentially feed nestlings that reach the highest in unparasitized nests. Because the height reached is size dependent, these findings also support Dearborn's (1998) size advantage hypothesis.

The results of the present study were essentially the same as those found for Yellow Warblers. Cowbird chicks in warbler nests begged more intensely, started begging sooner and reached higher than their host nestmates, with height rank being the single most important variable that determined which chick was fed (Lichtenstein and

Sealy 1998). Lichtenstein and Sealy's (1998) study, therefore, also supported the competition hypothesis, and more specifically, Dearborn's (1998) size advantage hypothesis. Lichtenstein and Sealy's (1998) study involved nests that contained only one cowbird chick and one warbler chick, whereas my study involved nests that contained normal brood sizes. The number of host chicks, therefore, does not affect the way in which hosts allocate food to parasitized broods.

In the absence of parasitism, height is an important variable that influences which chick is fed in a variety of species (Smith and Montgomerie 1991, Teather 1992, Leonard and Horn 1996, Dearborn 1998, Hofstetter and Ritchison 1998). Other factors also influence which chick is fed. These include being the largest nestling (Price and Ydenberg 1995), being the first to beg (Smith and Montgomerie 1991, Teather 1992, Leonard and Horn 1996, Dearborn 1998, Hofstetter and Richison 1998), occupying the favoured position in the nest, such as the central position (McRae et al. 1993) or the position closest to the parent (Smith and Montgomerie 1991, Teather 1992, Kilner 1995, Leonard and Horn 1996), extending the beak closest to the parent (Smith and Montgomerie 1991, Hofstetter and Richison 1998), having the reddest mouth colouration (Kilner 1997), and calling at the greatest rate and the loudest (Hofstetter and Richison 1998). In some species, males prefer feeding large nestlings and females prefer feeding small nestlings (Stamps et al. 1985, Leonard and Horn 1996). In most studies, either one factor was examined in isolation, or when multiple factors were considered, which, if any, most importantly influenced which chick is fed was ignored. More than one display may be used to improve the accuracy with which parents can assess the nutritional needs of their chicks ("backup signal" or "redundant signal hypothesis") (Johnstone 1996, Kilner and Johnstone 1997).

The competitive interactions between cowbird chicks and their hostmates have been examined in only one other study. Surprisingly, Dearborn (1998) did not find that

cowbird chicks reached higher than Indigo Bunting chicks. Nonetheless, he concluded that his study supported the size advantage hypothesis because he found support for some of the other predictions of this hypothesis. For example, cowbirds received more food than host chicks in Indigo Bunting nests, but not in Northern Cardinal nests where host nestlings are larger than cowbird nestlings. Dearborn (1998) also found support for the signal exaggeration hypothesis. For example, cowbirds may elicit feedings by begging for a longer period of time than buntings, begging sooner than buntings, and stopping begging later. Therefore, Dearborn's (1998) study supported the competition hypothesis, but it was unclear whether size advantage or signal exaggerations were more important in eliciting feedings because he did not determine which signals were most important in eliciting feedings in bunting nests.

There is no evidence that cowbird chicks used a supernormal stimulus to elicit feedings in this or any other study (Dearborn 1998, Lichtenstein and Sealy 1998). Although cowbirds occasionally fluttered their wings while begging in Indigo Bunting nests, a behaviour that was never exhibited by bunting nestlings, cowbirds were not more likely to be fed when they performed this behaviour (Dearborn 1998). Cowbird chicks did not exhibit any novel begging behaviours in Yellow Warbler nests (Lichtenstein and Sealy 1998). One component of the begging display that could potentially be a supernormal stimulus in catbird nests is gape colouration because cowbird nestlings have a red gape and catbird nestlings, like other mimid species, have an orange-yellow gape (Ficken 1965, Hinam 1998). In studies involving other species, parents preferred feeding nestlings with redder gapes (Kilner 1997) even if their young do not naturally have red gapes (Götmark and Ahlström 1997). Support for the supernormal stimulus hypothesis would have been if cowbirds were preferred regardless of whether they reached the highest, and nestling identify (i.e., cowbird or catbird) rather

than height rank would have been the most important variable to predict which nestling is fed in unparasitized nests. This was not the case.

Davies and Brooke (1989) concluded that another parasitic species, the Common Cuckoo, does not display a supernormal stimulus because when Reed Warblers (*Acrocephalus scirpaceus*) were presented with a choice between feeding a nest containing a cuckoo and a nest containing a brood of warblers, the cuckoo chick was not preferentially fed. Redondo (1993) found evidence that Great Spotted Cuckoos (*Clamator glandarius*) possess a supernormal stimulus because even though Black-billed Magpies (*Pica pica*) preferentially fed larger chicks in unparasitized broods, small cuckoo chicks were not disfavoured relative to larger magpie chicks. The cuckoo's white palatal papillae may act as a supernormal stimulus (Soler et al. 1995).

Cowbird chicks were fed twice as much food as catbird chicks even though they were not much larger than catbird chicks, so the *magnitude* of the size differential between cowbird and host nestmates does not influence the relative competitive ability of the cowbird chick. That a size differential exists at all is key to the preferential feeding of cowbird nestlings over their host nestmates. Adult cowbirds are only slightly larger than adult catbirds, so the relative timing of hatching has a large impact on the size hierarchy of cowbird chicks in catbird nests (Chapter 1, Figure 7). When a cowbird chick hatches *after* the catbird chicks, it is one of the smallest nestlings in the brood, which reduces its probability of survival because it is outcompeted by the larger catbird nestlings. On the other hand, when a cowbird chick hatches *before* catbird chicks, it becomes the largest nestling in the hierarchy, and is able to outcompete catbird chicks because it is able to reach higher. The cowbird's shorter incubation period (Briskie and Sealy 1990, McMaster and Sealy 1998), therefore, may have a substantial impact on the survival of cowbird nestlings, especially when parasitizing large hosts such as the catbird. Since cowbird chicks did not outcompete slightly larger Northern Cardinal

chicks (Dearborn 1998), catbird nestlings may be at the largest end of the mass continuum of host nestlings that cowbird nestlings can outcompete. Weatherhead (1989:365) commented that "cowbird nestlings appear to suffer no disadvantage" when competing with the larger Red-winged Blackbird nestmates, but he did not analyze nestling competition to substantiate this claim. I suspect that cowbird chicks were able to survive in the blackbird nests only when they were the first to hatch.

In addition to outcompeting catbird chicks, cowbird chicks are fed more than their host nestmates because they beg during a greater proportion of feeding visits (Dearborn 1998, this study). Cowbirds appear to have a high propensity to beg regardless of need. The cowbird's high propensity to beg may be due to their lack of relatedness to their nestmates and the adult provisioners. The lower the degree of relatedness, the greater the incentive for dishonest begging (Kilner and Johnstone 1997). Cowbirds are expected to demand a high level of parental care, even if it is at the expense of their nestmates or the future reproductive success of the provisioning adults. On the other hand, catbirds are not expected to demand a higher level of parental care than is necessary because they derive fitness benefits from the survival of their nestmates and their parents. Briskie et al. (1994) found a negative relationship between the loudness of begging calls and intrabrood relatedness.

Although some hosts of the cowbird have evolved the ability to recognize and eject foreign eggs, there are no records of a host rejecting parasitic nestlings of any species (Rothstein and Robinson 1998). Therefore, there is no need for cowbird chicks to evolve any specialized characteristics to increase their likelihood of being accepted or fed. For example, cowbirds do not mimic the begging calls of their hosts (Broughton et al. 1987). In a cross-fostering experiment, Eastzer et al. (1980) demonstrated that cowbird nestlings are not unique in their ability to elicit feedings from different species; however, as fledglings, cowbirds may be more successful at eliciting feedings from

different species than nonparasitic species. Cowbird fledglings are so successful at eliciting feedings from other species that Lorenzana and Sealy (1997) found 10 instances where cowbird fledglings were fed by individuals other than the original host (e.g., Woodward 1983, Klein and Rosenberg 1986). Many researchers have commented on the loud and persistent calling of the cowbird fledgling (e.g., Nice 1939, Woodward 1983, Klein and Rosenberg 1986). It should, however, be pointed out that nonparasitic species have also been recorded eliciting feedings from individuals other than the parents (reviewed by Shy 1982).

Effect of cowbird parasitism on food acquisition by catbird nestlings

Interestingly, although cowbird nestlings enjoyed a much greater chance of being fed than catbird nestlings, the number of feedings obtained by core and marginal catbird nestlings in parasitized and unparasitized nests did not differ significantly. The increase in overall provisioning rates by the female catbird (Chapter 2) compensated for the extra feedings obtained by the cowbird nestling. With Indigo Buntings, Dearborn et al. (1998) did not find that the increase in provisioning rates by host adults compensated for the disproportionate amount of food obtained by the cowbird nestling.

It is interesting that catbird nestlings did not increase their begging intensity even more than they did. By extending their tarsi in addition to stretching their necks, they should have been able to reach higher than the cowbird nestling, and been successful in outcompeting the cowbird (assuming that the cowbird nestling would not have responded to the catbird nestlings' extra height by also extending its tarsi). In other species, the height to which a nestling reaches depends on hunger (Smith and Montgomerie 1991, Kacelnik et al. 1995). Energetic constraints should not limit the catbird nestlings from extending their tarsi (Bachman and Chappell 1998, Chappell and Bachman 1998). The energetic costs of begging are relatively low in three other

species, requiring only 5 to 28% more energy than resting (Leech and Leonard 1996, McCarty 1996, Bachman and Chappell 1998). If catbird chicks in parasitized nests were energetically stressed (i.e., in need of food), I predict that they would have begged during all of the feeding visits. Instead, they only begged during 60% of the feeding visits, which is less frequently than cowbird chicks.

In summary, the findings of this study parallel those of other studies (Dearborn 1998, Lichtenstein and Sealy 1998) in that cowbird chicks do not use "supernormal" traits to sequester more food than their host nestmates. Brown-headed Cowbirds are simply good at outcompeting their hosts because they are able to reach higher as a result of their larger size, and many species preferentially feed nestlings that reach the highest. Although cowbirds were preferentially fed, catbird chicks in parasitized and unparasitized nests received the same amount of food due to an increased feeding rate by adult catbirds.

SUMMARY

1. Gray Catbirds did not eject conspecific eggs introduced into their nests.
2. No evidence of natural conspecific brood parasitism was detected in catbird nests.
3. The cost to catbirds of ejection was 0.01 catbird eggs per ejection attempt, which is the equivalent of 0.0022 catbird fledglings per ejection attempt.
4. Parasitized nests fledged an average of 0.63 fewer chicks than unparasitized nests.
5. The recoverable cost of parasitism for Gray Catbirds (0.63 fledglings) was greater than the cost of ejection (0.0022 fledglings).
6. Catbird nestlings in parasitized nests were smaller than catbird nestlings in unparasitized nests, but this difference was not significant.
7. Adult female catbirds had a higher feeding rate at parasitized nests than at unparasitized nests; males did not.
8. Cowbird chicks obtained twice as much food as catbird chicks because cowbird chicks begged more often than catbird chicks and catbird adults preferentially fed cowbird chicks.
9. The height rank was the single most important parameter that determined which nestling, cowbird or catbird, was offered food first.
10. Cowbird nestlings were larger, begged sooner and reached higher than catbird nestlings.
11. Cowbird chicks were preferentially fed by catbird adults because they reached higher than catbird chicks, and not through the use of a supernormal stimulus.
12. Catbird chicks in parasitized nests begged more often and more intensely than catbird chicks in unparasitized nests.

13. The increase in feeding rate by female adults compensated for the presence of a cowbird chick; therefore, catbird chicks in parasitized and unparasitized nests received the same number of feedings per hour on days 4 and 5 post-hatch.

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Appendix 1. Source of Brown-headed Cowbird chicks placed into Gray Catbird nests.

Source of cowbird egg ¹	Number of cowbird chicks placed into catbird nests (%)		
	1997	1998	Total
Gray Catbird	1 (10)	0 (0)	1 (2.5)
Yellow Warbler	4 (40)	16 (53)	20 (50)
Song Sparrow	2 (20)	5 (17)	7 (17)
Clay-colored Sparrow	0 (0)	1 (3.3)	1 (2.5)
Red-winged Blackbird	0 (0)	3 (10)	3 (7.5)
Captive female cowbird	3 (30)	5 (17)	8 (20)
Total	10	40	

¹ Scientific names of species not mentioned in text: Song Sparrow, *Melospiza melodia*;
Clay-colored Sparrow, *Spizella pallida*.

Appendix 2. Correlation between tarsus length and mass in Gray Catbird chicks on days 1 to 8.

Day	Pearson correlation
1	0.73
2	0.88
3	0.90
4	0.90
5	0.87
6	0.85
7	0.83
8	0.78

Appendix 3. Mean clutch size for Gray Catbird nests.

Year	Mean clutch size \pm SE	Number of nests
1996	4.5 \pm 0.6	31
1997	4.4 \pm 0.6	98
1998	4.4 \pm 0.6	100
Overall	4.4 \pm 0.6	229

Appendix 4. The stage naturally parasitized Gray Catbird nests were parasitized and the outcome of the model cowbird egg that replaced the real egg.

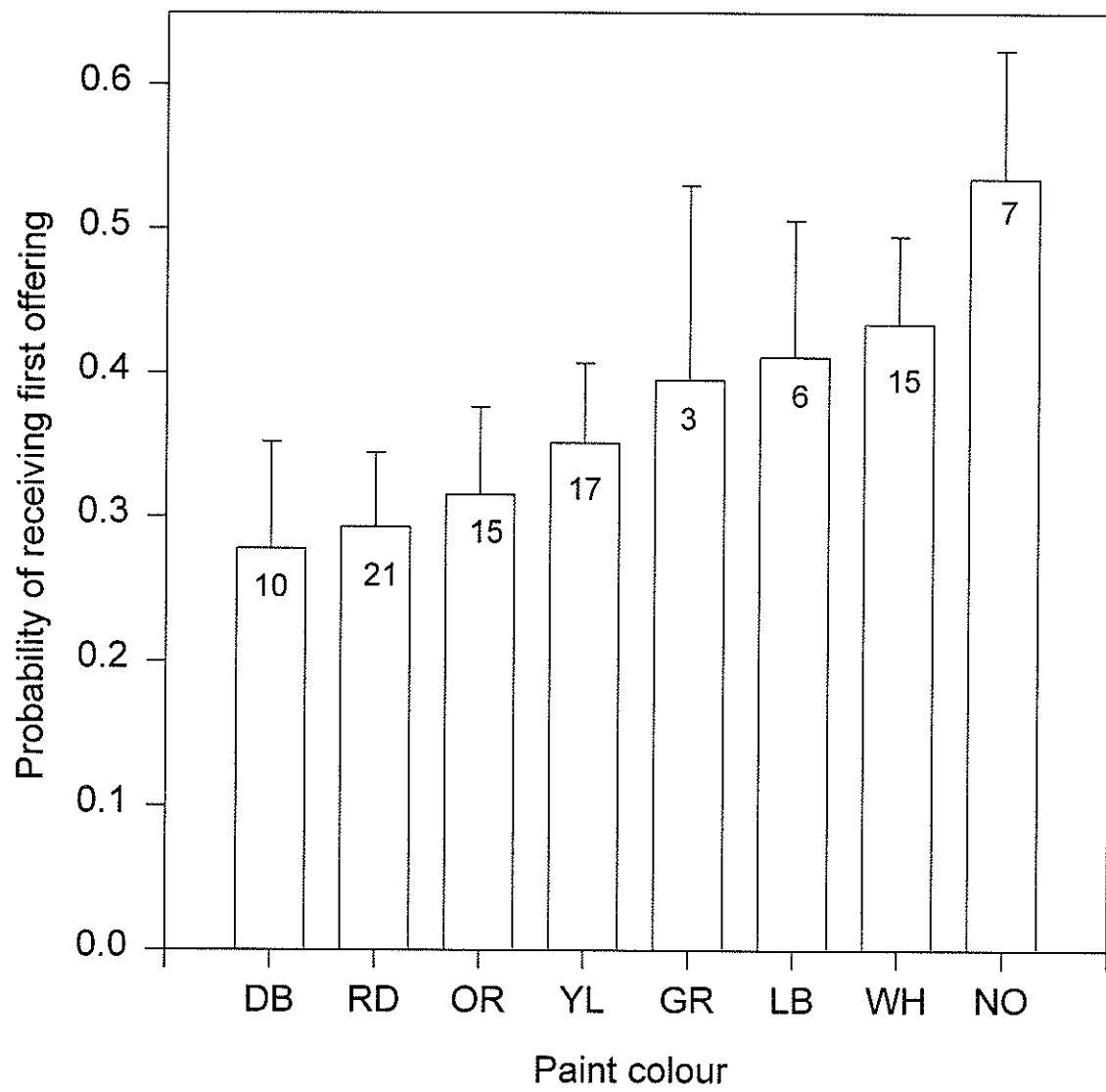
Nest number	Day nest parasitized ¹	Outcome of cowbird egg
GC-96-6	On or before LD2	Ejected between 3 and 4 days
GC-96-21	LD1 or LD2	Nest deserted on LD3
GC-96-33	Unknown because nest found during incubation	Depredated two days after nest found
GC-97-40	On or before LD2	Ejected within 1 day
GC-97-C15	On LD3	Ejected between 1 and 2 days

¹ The precise day a nest was parasitized was not known if a nest contained a cowbird egg when found or if a nest was not inspected daily.

Appendix 5. Effect of the dummy video camera on the probability of Gray Catbirds being visibly agitated while they were being videotaped. Eighty percent of the catbirds at nests that did not receive a dummy video ($n = 45$) and 83% of the catbirds at nests that received a dummy video treatment ($n = 12$) were not bothered by the video camera. (See p. 47 for characteristics of catbird pairs that were bothered by the video). The use of a dummy video did not affect the probability of the catbirds being disturbed by the video camera (Fisher's exact test, $P = 1.00$).

Appendix 6. Effect of the colour used to paint the heads of Gray Catbird and Brown-headed chicks on the competitive ability of the chicks. Upon returning to the nest, some adults picked at the paint on the chick's heads, especially when the paint was white and, to a lesser extent, yellow. This may be because the parents mistake the white paint for a fecal sac. The effect of paint colour did not have a significant effect on the probability of being offered a first feeding ($F= 1.44$, $df = 7, 84$, $P = 0.20 > 0.017$, Power = 57.7%) when height rank and beak rank were used as covariates. Nonetheless, nestlings without paint and those painted white seemed to have a particularly high probability of being offered food first and nestlings painted dark blue and red had a low probability of being offered food (Appendix 7).

Appendix 7. The effect of head colour on the probability that begging catbird and cowbird chicks will receive the first food offering. Paint colours: DB, dark blue; RD, red; OR, orange; YL, yellow; GR, green; LB, light blue; WH, white; NO, no paint. Sample sizes are indicated in the bars. Error bars = standard error.



Appendix 8. Significance of the mean difference between the number of feedings obtained per hour in Gray Catbird nests using Tukey's method.

	Cowbird nestling	Core in parasitized nest	Marginal in parasitized nest	Core in unparasitized nest
Core in parasitized nest	0.004*	-	-	-
Marginal in parasitized nest	0.026*	0.998	-	-
Core in unparasitized nest	0.003*	0.945	0.999	-
Marginal in unparasitized nest	0.010*	0.891	0.991	0.998

* $P \leq 0.05$.

Appendix 9. Significance of the mean difference between the probability of obtaining a first food offer in Gray Catbird nests using Tukey's method.

	Cowbird nestling	Core in parasitized nest	Marginal in parasitized nest	Core in unparasitized nest
Core in parasitized nest	0.029*	-	-	-
Marginal in parasitized nest	0.177	0.184	-	-
Core in unparasitized nest	0.303	0.139	0.158	-
Marginal in unparasitized nest	0.046*	0.145	0.164	0.111

* $P \leq 0.05$.

Appendix 10. Significance of the mean difference between start rank in Gray Catbird nests using Tukey's method.

	Cowbird nestling	Core in parasitized nest	Marginal in parasitized nest	Core in unparasitized nest
Core in parasitized nest	0.786	-	-	-
Marginal in parasitized nest	0.037*	0.291	-	-
Core in unparasitized nest	0.135	0.803	0.670	-
Marginal in unparasitized nest	0.414	0.989	0.385	0.941

* $P \leq 0.05$.

Appendix 11. Significance of the mean difference between height rank in Gray Catbird nests using Tukey's method.

	Cowbird nestling	Core in parasitized nest	Marginal in parasitized nest	Core in unparasitized nest
Core in parasitized nest	0.014*	-	-	-
Marginal in parasitized nest	0.217	0.877	-	-
Core in unparasitized nest	0.017*	0.946	0.991	-
Marginal in unparasitized nest	0.011*	0.995	0.953	0.994

* $P \leq 0.05$.

Appendix 12. Significance of the mean difference between tarsus length in Gray Catbird nests using Tukey's method.

	Cowbird nestling	Core in parasitized nest	Marginal in parasitized nest	Core in unparasitized nest
Core in parasitized nest	0.009*	-	-	-
Marginal in parasitized nest	< 0.0005*	0.153	-	-
Core in unparasitized nest	< 0.0005*	0.975	0.213	-
Marginal in unparasitized nest	< 0.0005*	0.005*	0.988	0.002*

* $P \leq 0.05$.

Appendix 13. Excluded variables in the stepwise regression model involving the probability of being offered the first feeding when a Brown-headed Cowbird chick was not present in Gray Catbird nests.

Excluded variable	t-value	P-value
Height rank	-1.911	0.078
Start rank	1.175	0.261
Beak rank	-0.986	0.342
Begging intensity	-0.179	0.860
Tarsus length	-0.488	0.835
Mass	0.187	0.854

Appendix 14. Excluded variables in the stepwise regression model involving the probability of being offered the first feeding when a Brown-headed Cowbird chick was present in Gray Catbird nests.

Excluded variable	t-value	P-value
Mass	1.023	0.330
Tarsus length	0.866	0.407
Begging intensity	0.588	0.570
Beak rank	-0.206	0.840
Start rank	0.078	0.940
Catbird or cowbird nestling	0.051	0.960

Appendix 15. Correlations between begging parameters and the probability of receiving a first offer in unparasitized Gray Catbird nests.

	Prob. first offer	Tarsus length	Mass	Start rank	Height rank	Beak rank
Tarsus	-0.082	1.000	-	-	-	-
Mass	-0.018	0.934	1.000	-	-	-
Start rank	-0.157	0.034	0.109	1.000	-	-
Height rank	-0.366	-0.249	-0.230	0.752	1.000	-0.270
Beak rank	-0.063	0.450	0.449	0.111	-0.270	1.000
Begging intensity	0.061	-0.241	-0.324	0.156	0.063	-0.145

Appendix 16. Correlations between begging parameters and the probability of receiving a first offer in parasitized Gray Catbird nests.

	Prob. first offer	Tarsus length	Mass	Start rank	Height rank	Beak rank	Begging intensity
Tarsus	0.679	1.000	-	-	-	-	-
Mass	0.633	0.905	1.000	-	-	-	-
Start rank	-0.726	-0.502	-0.456	1.000	-	-	-
Height rank	-0.915	-0.654	-0.581	0.801	1.000	-	-
Beak rank	-0.761	-0.302	-0.227	0.705	0.815	1.000	-
Begging intensity	0.406	-0.231	-0.121	-0.536	-0.368	-0.458	1.000
Species	0.703	0.802	0.748	-0.634	-0.764	-0.451	0.065